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HUMAN EMBRYOLOGY AND MORPHOLOGY

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HUMAN EMBRYOLOGY AND MORPHOLOGY

BY

ARTHUR KEITH

M.D., F.R.S., LL.D. (ABERDEEN), F.R.C.S. (ENG.)

CONSERVATOR OF THE MUSEUM AND HUNTERIAN PROFESSOR
ROYAL COLLEGE OF SURGEONS, ENGLAND

FULLERIAN PROFESSOR IN COMPARATIVE ANATOMY, ROYAL INSTITUTION, LONDON

*FOURTH EDITION, REVISED AND ENLARGED
WITH NEARLY 500 ILLUSTRATIONS*

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1921

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PREFACE TO FOURTH EDITION

THE issue of a new edition has given the author an opportunity not only of incorporating recent additions to our knowledge of the development and morphology of the human body, but also of recasting many of the chapters. Over eighty new illustrations have been added. The chief alterations relate to sections dealing with the origin of the foetal membranes, the growth of the embryo and foetus, and the nature of the basal ganglia of the brain. The chapters dealing with the pharynx, the ear, the heart, and the lymphatic system have been rearranged and to a large extent rewritten. The enquiries of the late Professor Franklin P. Mall have shown that human embryos, in their earlier stages, are a week older than was formerly believed. The estimated ages of embryos now given in this work are based on Professor Mall's calculations.

Experience has confirmed the author in his earlier opinion that the facts of embryology are barren and meaningless until they are interpreted in the light of our knowledge of the evolution of the human body—a knowledge which must be founded on a comprehensive survey of comparative anatomy and physiology. Hence in this new edition the author has sought to give, not only a descriptive history of the development of the various systems of the body, but to make the facts intelligible by bringing a knowledge of comparative anatomy and evolution to bear on them.

Human Embryology and Comparative Anatomy have become vast fields of knowledge. Here they are dealt with only in so far as they bear directly on the nature of the human body, and reflect what the author has found to be useful in the course of his daily work and teaching. Every effort has been made to make the book representative of the latest British Research.

In the preparation of the present edition the author has become indebted to a very wide circle of friends too numerous to be mentioned individually. He cannot, however, allow the occasion to pass without a warm acknowledgment of his indebtedness to Dr. Alexander Low, Lecturer on Embryology in the University of Aberdeen, for the help he has given.

ARTHUR KEITH.

ROYAL COLLEGE OF SURGEONS OF ENGLAND,
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HUMAN EMBRYOLOGY AND MORPHOLOGY.

CHAPTER I.

EARLY CHANGES IN THE DEVELOPMENT OF THE OVUM AND EMBRYO.

The First Five Weeks of Development.—In the first five weeks of human development changes take place very rapidly. In that short

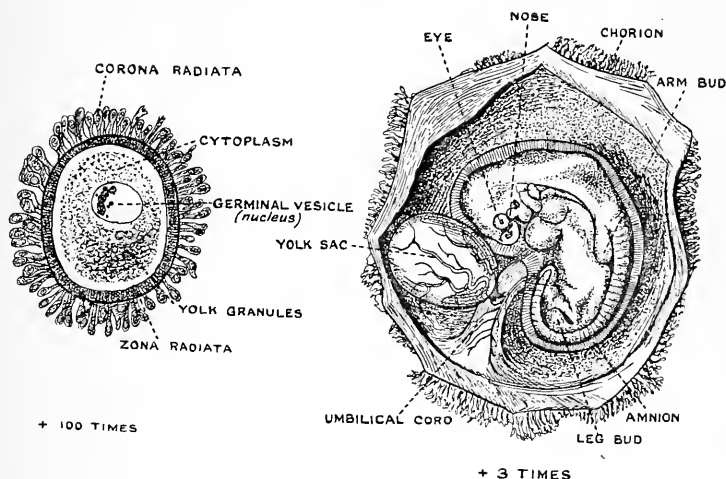


FIG. 1.—The parts of a Mature Human Ovum. (After Van der Stricht.)

FIG. 2.—Human Embryo and its Membranes at the end of the fifth week of development. (After Kollmann.)

time the fertilized ovum passes from the condition of a single cell, with a diameter of $\frac{1}{250}$ of an inch¹ to a fully formed human embryo about $\frac{1}{5}$ of an inch in length (5 mm.), and contained within a spherical envelope of embryonal membranes which measures nearly an inch in diameter (see Figs. 1 and 2). By the end of the fifth week the beginnings of all the

¹ Measurements are given at first according to our English standard, but throughout this book the more convenient metric system will be employed. One inch = 25.4 mm. One millimetre = 1000 μ , or micromillimetres, or mikrons.

parts of the adult body are recognizable—the head, the trunk, the limbs, the primitive segments, the eyes, the nose and mouth. A section across the abdominal cavity of an embryo at this stage (see Fig. 23) reveals the fact that the foundations of the genital glands are already laid, and that certain cells have been set aside for the reproduction of another generation. Thus by a cycle of developmental changes a new generation of reproductive cells has been produced from the fertilized ovum of a former generation all taking place within the short space of five weeks. In this chapter we are to follow the changes which lead from the fertilized egg or oocyte of

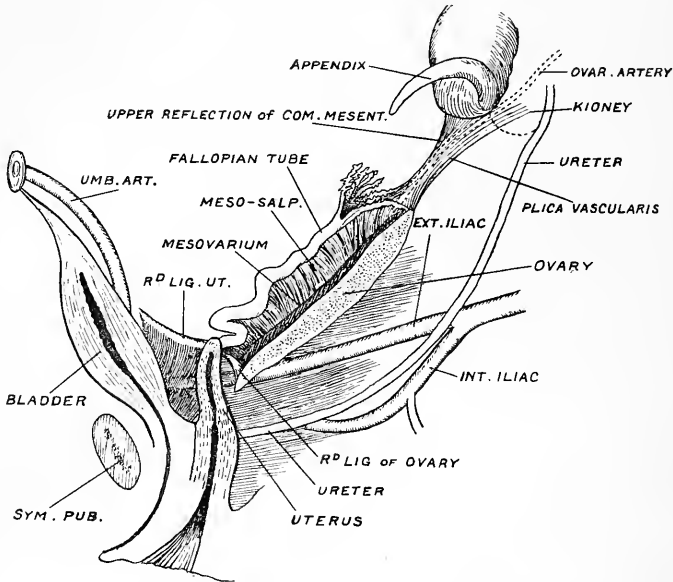


FIG. 3.—The position of the Ovary and Fallopian Tube in the 5th month.

the mother to the establishment of a new brood of genital cells in the embryo. In this way life is handed on from one generation to another.

Descent of the Ovary.—In tracing the cycle of changes which lead from the fertilized ovum of one generation to the production of a reproductive gland in the next generation, we may begin our study at any point, but for many reasons it is convenient to commence with the condition of the ovary in a fifth-month foetus. The ovary is descending or migrating from the region of the kidneys where it was formed, and has reached the iliac fossa. In all primitive vertebrate animals the genital glands are stationed above the kidneys, but in mammals, for reasons to be explained afterwards, they descend to the lower part of the trunk—a change which is especially well seen in the human subject. In the fifth month the ovary is long and narrow, with an upper or cranial and lower or caudal pole; it is three-sided in section—the surfaces being medial, lateral and inferior or ventral (Fig. 3). The Fallopian tube or oviduct lies along the outer side of the ovary in the iliac fossa; its upper

fimbriated end terminates at, and is attached to, the upper or cranial pole of the ovary (Fig. 3). As the parts lie on the iliac fossa, the tube and the ovary are supported each by its own mesentery, the **mesosalpinx** and **mesovarium**. The two mesenteries have, however, a common origin or attachment to the posterior abdominal wall, and to the common attachment the name of **common genital mesentery** may be given (Fig. 4). The upper end of the common mesentery—the **plica vascularis** (Fig. 3), as it is reflected from the cranial pole of the ovary and fimbriated extremity of the tube, is continued up towards the diaphragm and in it the ovarian vessels and nerves pass to the ovary and tube. The caudal pole of the ovary is joined to the uterus by its round ligament. The round ligament

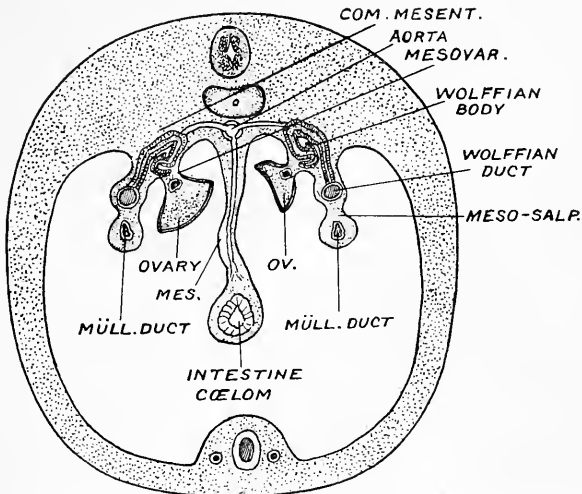


FIG. 4.—Diagrammatic Section of a Foetus at the beginning of the 3rd month (30 mm. long), showing the attachments of the Ovary and Müllerian duct.

of the uterus, corresponding to the gubernaculum testis of the male, passes from the brim of the pelvis, where it is attached to the horn of the uterus, almost straight to the internal inguinal opening and assists in the descent of the ovary and tube.

By full term the ovary lies at the brim of the pelvis or partly within it; after birth the ovary, uterus and rectum come gradually to occupy their adult positions within the pelvis. This is due to a relatively great growth in the pelvis, which becomes marked as the child learns to walk, and especially in the female at the time of puberty. The ovary, as is more frequently the case with the testicle, may be arrested in its descent.

In Fig. 4 an **earlier stage** is shown; it represents the condition about the beginning of the third month. The ovary and tube with the remnants of the Wolffian body—a primitive form of kidney—occupy the position in which they are developed. Both are suspended by mesenteries from the dorsal wall of the peritoneal cavity, at the side of the mesentery of the gut.

Normal Position of the adult Ovary.—When the ovary descends within the pelvis it usually occupies a definite triangle—the **ovarian triangle**—on the lateral wall of the pelvic cavity (Fig. 5). The ovarian triangle is bounded above by the upper half of the external iliac artery, below and behind by the internal iliac artery, with the ureter lying on the artery; in front by the reflection of the posterior layer of the broad ligament on the side of the pelvis. The peritoneum covering the triangle forms a depression, or occasionally a pouch, for the ovary. The fimbriated end of the Fallopian tube is applied to the ovary, ready to receive the ripe ova and transfer them to the uterus. One of the fimbriae—the ovarian fimbria—tethers the tube to the ovary. It will be seen that, with the descent of the ovary, the mesosalpinx, the mesovarium, and the common

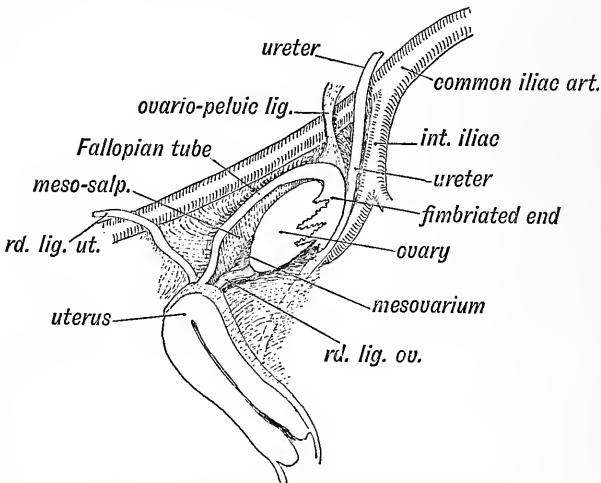


FIG. 5.—Showing the position of the Ovary on the lateral wall of the Pelvis and its relation to the Fallopian Tube.

genital mesentery have come to form the major part of the broad ligament. The upper end of the common genital mesentery now forms the ovario-pelvic ligament (Figs. 3 and 5). The ovary brings down with it, too, the ovarian arteries, veins, lymphatics and plexus of nerves. The nerves come through the aortic plexus from the 10th and 11th dorsal segments of the spinal cord, and the lymphatic vessels carry the ovarian lymph to a group of glands situated high up in the lumbar region.

An Ovum.¹—As the infantile ovaries descend, each is laden with thousands of ova (over 10,000, T. G. Stevens; 100,000, F. H. A. Marshall). It is estimated that not more than 200 in all become ripe and are shed. The ova are embedded in the stroma of the ovary, each being surrounded by a special company or cluster of epithelial cells, which provide both

¹ For fuller details and literature see Francis H. A. Marshall, *The Physiology of Reproduction*, London, 1910. For more recent investigations on the maturation of Graafian follicles in Man see Prof. Arthur Thomson, *Journ. of Anat.* 1919, vol. 53, p. 172, vol. 54, p. 1. See also Prof. Arthur Robinson, *Trans. Roy. Soc. Edin.* 1918, vol. 52, p. 303.

a nest and nourishment for the ovum or oocyte (Figs. 6, 7). The cells which surround an ovum, with a condensed layer of the stroma cells outside them, form a **Graafian follicle**. As the ovary descends it is covered by a cubical epithelium, derived from the **germinal epithelium** which formed a stratum on the free surface of the ovary at its first appearance in the roof of the abdominal cavity. The ova and their accompanying **follicular cells** are derived from the surface stratum. Amongst the columnar cells of the germinal epithelium and also in the stratum immediately beneath them are large peculiar cells. These are the **primordial ova** from which brood ova arise. The ova are thus carried within the ovary by ingrowths of the germinal epithelium. These tubular invasions into the ovary become broken up, the isolated masses of the germinal epithelium remaining to form the linings of the Graafian follicles. In the outer or cortical zone follicles continue to form in early foetal life, but after birth and even to the

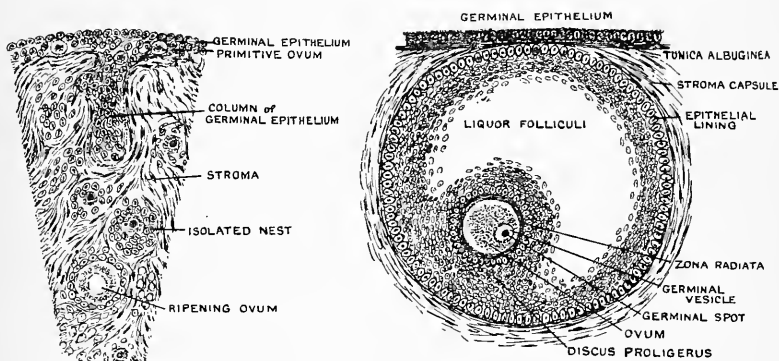


FIG. 6.—Diagrammatic Section of the Ovary of a fifth month Foetus, showing Nests of Germinal Epithelium and unripe Graafian Follicle.

FIG. 7.—Ripe Graafian Follicle at Puberty.

end of the fifth decade of a woman's life, follicles are being continually formed. With this new formation there is an equally constant process of degeneration or atresia of follicles. We shall see that another important constituent of the ovary also arises from the tubular incursions of the germinal epithelium—namely the **interstitial cells**, which are glandular in nature, and supply an internal secretion which has much to do with the growth and regulation of the sexual structures of the body.

Discharge of the Ova.—At puberty especially, also before it, and for 30 years after it, one egg after another ripens; the ovum enlarges; so does its Graafian follicle (Fig. 7). The cells of the epithelial lining proliferate and a cavity appears within the follicle, due to a collection of fluid—the liquor folliculi—amongst the cells. The ovum remains attached to the wall of the follicle by a group of epithelial cells, the discus proligerus or cumulus (Fig. 7). As the fluid collects, the follicle works its way to the surface of the ovary; the tunica albuginea, which forms a capsule for the ovary, and the covering epithelium, gradually atrophy over it, and at last it bursts and discharges the ovum.¹ Ova may be shed

¹ As to the mechanism of rupture, see references given on p. 4.

at any point of a woman's menstrual cycle but the most usual time is during or just after the menstrual period. All the circumstantial evidence at our disposal points to the 10th or 11th day of a menstrual cycle, counting from the first day of the menstrual flow, as being the most common for conception. Whether ova are discharged from both ovaries at once, or from only one, and whether one or more than one in a month, are points not yet settled; but the usual opinion is that one ovum is shed each month, and only from one ovary. An ovum shed from one ovary may occasionally pass down by the opposite Fallopian tube.

The Graafian follicle, after rupture, fills up with blood; a cellular tissue is soon developed within its cavity from the lining cells of the follicle but particularly from cells of the inner sheath of the follicle. The inner sheath cells break into the follicle and carry blood vessels with them. These cells come to contain lutein, which gives them a yellowish colour when seen in the mass. If pregnancy does not occur, a **false corpus luteum** is formed, a formation which begins to disappear before the next menstrual period. If pregnancy occurs, however, the cellular mass continues to increase in size until it forms a glandular body as large as a pigeon's egg and is known as a **true corpus luteum**. It reaches its maximum size about the fourth or fifth month of pregnancy; it is much reduced in size by the end of that period. Experiments have been made by Marshall and Jolly and by Blair Bell which show that the secretion of the corpus luteum acts on the decidual or lining membrane of the uterus, sensitizing it so that it responds by growth when the fertilized ovum comes in contact with the decidua. If the corpus luteum is excised pregnancy is prevented, or if begun, is arrested. Both forms of corpus luteum lead to the formation of cicatrices which are to be seen on the surface of the ovary. The ovary of an old person is commonly covered with such scars. The Graafian follicles may become cystic and give rise to enormous ovarian tumours.

The Fallopian Tube.—When the ovum or oocyte drops from the ovary it cannot easily escape the ciliated fimbriae of the Fallopian tube which surround and clutch the ovary. In Fig. 5 the relationship of the Fallopian tube to the ovary is shown. The tube may be demarcated into three parts: (a) the isthmus or arm directed outwards to the wall of the pelvis ($\frac{1}{2}$ to 1 inch); (b) the forearm or ampullary part, directed backwards on the lateral pelvic wall above the ovary; (c) the hand, infundibular, or fimbriated part, folded backwards and grasping the free border and exposed surface of the ovary. The tube is fastened by one of its fimbriae to the cranial pole of the ovary.

Course of the Ovum in the Tube.—The cilia on the fimbriae work towards the ostium abdominale, the abdominal mouth of the Fallopian tube, which is situated at the bases of the fimbriae, and carry the discharged ovum through the ostium within the tube. The ostium abdominale is shut when the tube is examined after excision; the closure is probably due to reflex contraction of the tube muscle, caused by handling and cutting. In the infundibular and ampullary segments of the tube, the mucous membrane is thrown into long plicated folds shown in section in Fig. 8. They are covered with ciliated epithelium, which urge the ovum

towards the uterus. Between these folds, in the upper reach of the tube, the ovum, if it is to be fertilized, usually meets the male cell or spermatozoon, for we know that spermatozoa can remain alive in the tube for at least seven days after connection. The passage of the fertilized ovum along the tube takes place slowly for it undergoes its first developmental changes during this journey which is supposed to extend over a period of four or five days. If the passage of the fertilized ovum is obstructed, which may result from an inflammation or cicatrization of the epithelial lining of the tube, development may proceed at the point of obstruction.¹ When **tubular pregnancy** occurs, the growing ovum expands and ultimately perforates the tube—usually in the second month—an accident which is always attended by a grave haemorrhage.

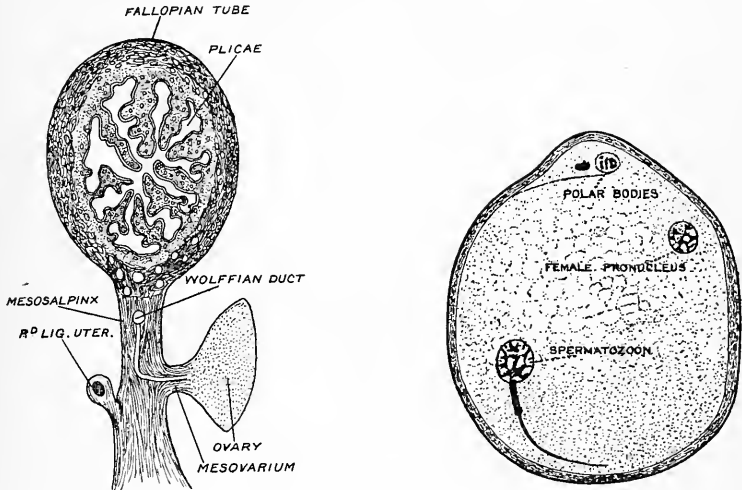


FIG. 8.—Diagrammatic Section of the Broad Ligament and Fallopian Tube.

FIG. 9.—Mature Ovum of Bat, showing the separated Polar Bodies, the Female Pronucleus and a Spermatozoon about to form a Male Pronucleus. (After Van der Stricht.)

The History of the Ovum within the Fallopian Tube.—When the ovum enters the Fallopian tube, it is a cell of very considerable size (100μ) with a cell wall—the **zona radiata** (Fig. 1), a nucleus—the **germinal vesicle**, and a nucleolus—the **germinal spot**. Then, or before then,² the ovum prepares for fertilization by the extrusion from its nucleus of first one, then a second **polar body**, and, with the extrusion, the germinal vesicle becomes the **female pronucleus** (Fig. 9). The polar bodies or polocytes, for they really represent cells, lie outside the protoplasm of the ovum, but within the zona radiata; they are parts of the germinal vesicle which are extruded with all the display of karyokinesis—the peculiar

¹ See F. P. Mall, *Surg. Gynaec. and Obstet.* 1915, vol. 21, p. 289.

² Prof. Arthur Thomson has shown that ova are to be seen in the human ovary with both polar bodies already extruded and that maturation changes can be seen to take place before the ova are shed, *Journ. Anat.* 1919, vol. 53, p. 172.

changes manifested by the nucleus when a cell is about to divide. We shall see that the three polar bodies really represent three aborted ova—which have left their cell bodies to enrich the principal ovum.

Karyokinesis.¹—The preparatory or maturation changes which take place in the nucleus of the ovum and also in the nucleus of the male germinal cell are of the greatest interest to us, for we have good grounds for suspecting that the mechanism which regulates the shaping of the adult body is represented in the substance of the nucleus of the germ cell. The nucleus appears to be the chief vehicle of heredity—the medium by which the features of the parent are handed on to the child. Hence the importance attached by embryologists to the elaborate changes undergone by the nucleus of a maturing male or female germ-cell. When an ordinary cell of the body is about to divide, the nucleus undergoes certain

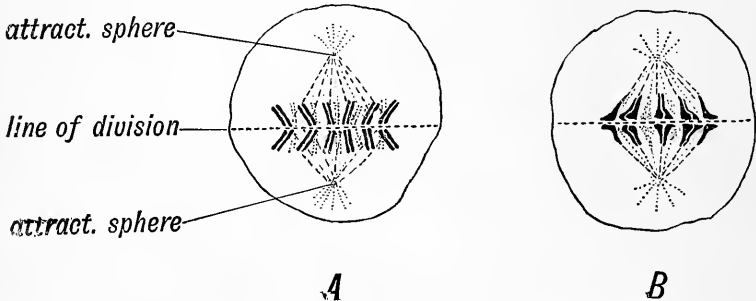


FIG. 10, A.—Diagram of Karyokinesis in a somatic cell (homotypical division).

B.—Diagram of Karyokinesis during the production of matured ova and spermatozoa (heterotypical division). (After J. B. Farmer.)

changes before cleavage takes place. The nuclear division precedes that of the whole cell. This mode of cell division or cell propagation is known as Karyokinesis or Mitosis. Two elements within the nucleus play a part in the process—the **chromatin**, which readily combines with certain staining reagents, and the **achromatin**, which does not absorb dyes. In the resting phase, the chromatin is scattered as minute particles in the substance of the nucleus, but when mitosis is to take place the particles unite into filaments; the filaments break up into segments or rods, each rod being known as a **chromosome** (Fig. 10). The number of chromosomes appearing in each somatic cell is approximately constant for each species of animal; in man twenty-four is the usual number (Broman). As the chromosomes form, an achromatin formation appears in the substance of the cell body just outside the nucleus—the **centrosome**, which appears to yield a commanding influence on the division of the nucleus. The centrosome divides; the two halves move apart until they lie at opposite poles of the nucleus where each forms an **attraction sphere** (Fig. 10). The attraction spheres become joined by a **spindle** of achromatin threads, the chromosomes of the nucleus

¹ For literature and significance of Mitosis see C. E. Walker, *Essentials of Cytology*, London, 1907; Bashford and Murray, "Significance of Mitosis," *Proc. Roy. Soc.* 1904, vol. 73, p. 66; R. Fick, *Ergebnisse der Anat.* 1906, vol. 16, p. 1; S. Tschassownikow, *Anat. Hefte*, 1911, vol. 45, p. 197; Prof. W. E. Agar, *Cytology*, 1920; Prof. F. R. Lillie, *Fertilization of the Ovum*, 1919,

then appearing as if they were supported by the spindle between the attraction or centrospheres. The chromosomes move towards the equatorial plane of the nucleus—midway between the attraction spheres; during the movement each chromosome divides longitudinally, so that each is split into two, the two halves lying side by side, often bent into V-shaped forms (Fig. 10, *A*). As the nucleus divides in the equatorial plane 24 chromosomes pass into one half and 24 into the other. The attraction spheres fade away; the division of the cell body is completed, each half having now its own nucleus; the chromosomes break up in the network of the daughter nuclei and the two cells enter a resting phase. By this means an equitable distribution of the chromatin material of the parent nucleus is made to the two daughter cells.

The two karyokinetic divisions undergone by the ovum before fertilization differ in three particulars from the process as seen in a somatic cell: (1) Only 12 chromosomes are formed—each being really double; (2) the chromosomes are peculiar in shape and in manner of division (Fig. 10, *B*); (3) the cell body divides very unequally—only a very minor part accompanying that half of the nucleus which is separated at the first and second divisions of the ovum and which form, when thus separated, the first and second polar bodies or polocytes. A division of the first polar body accompanies the separation of the second polar body from the ovum, there being thus three polocytes formed during the maturation of the ovum. Thus the two divisions undergone by the ovum result in the formation of one matured ovum and three polocytes. Three-fourths of the chromatin in the nucleus of the original ovum are extruded in the polar bodies. The number of chromosomes in the ripe ovum has been reduced from 24 to 12.

The cells of a malignant tumour frequently show in their divisions the peculiar mitotic changes which are seen in the preparation of the female pronucleus. Prof. J. B. Farmer regards such cells as essentially germinal in character. It has also been found that the heterotypical or reducing form of mitosis may occur in leucocytes and in inflamed tissues.

Formation of Spermatozoa.—Having thus described the maturation of the ovum, and followed it within the Fallopian tube, it is necessary to trace the history of its counterpart in the male—the spermatozoon. The manner in which a spermatozoon is produced by a primary and secondary division from a **spermatocyte** is very similar to the production of a **mature** from an **immature** ovum. The form of mitosis is the same (heterotypical), the chromosomes being reduced to 12 in number and to a peculiar shape. The two divisions take place within the seminiferous tubules of the testis, and result in the production of four spermatozoa—corresponding to the matured ovum and three polar bodies (Fig. 11, *B*). The seminiferous tubules correspond to the ingrowths of germinal epithelium which carry the primordial ova within the ovary. Lining the tubules are two kinds of cells—those of Sertoli (Fig. 11, *B*), large cells for nourishing the spermatozoa—representing those of the stratum granulosum in the Graafian follicles—and other cells known as spermatogonia, corresponding to primordial ova. Spermatogonia divide and give rise to primary

spermatocytes which correspond to immature ova. A primary spermatocyte divides into two secondary spermatocytes, each of which again divides and thus four cells are produced, which become modified into spermatozoa (Fig. 11, *B*). The nucleus forms the head, the junctional part represents the centrosome,¹ while the tail is all that remains of the substance of the cell body (Fig. 11, *A*). While the ripe ovum has a diameter of 100μ ($\frac{1}{30}$ th in.) the total length of a spermatozoon is only 50μ . While the ovum represents a large passive cell, laden with nourishment or yolk, its male counterpart becomes highly modified within the Sertoli or nurse cell, has its cell substance reduced to a minimum and is given a power of active motion. While ova are ripened singly, spermatozoa ripen by the million. Gemmill has shown that spermatozoa can be kept

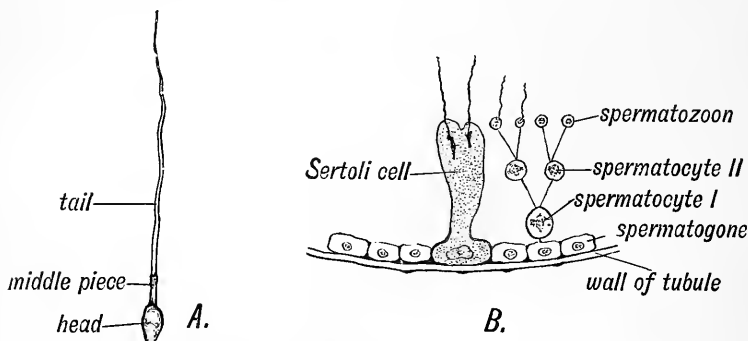


FIG. 11, *A*.—Diagram of a Spermatozoon.

B.—Diagram showing the origin of Spermatozoa from the lining cells (spermatogonia) of the tubules of the testicle.

alive for many days in nutritive media; probably the secretions of the epididymis, vesiculæ seminales, prostate and Cowper's glands are for this purpose.

Fertilization.—In the course of fecundation thousands of spermatozoa are lodged in the genital passage; many stem the adverse current of the uterine cilia, reach and live for days within the interlaminae grooves in the wider parts of the tube.² In the course of its descent within one of the grooves the egg may be fertilized. The spermatozoon, attracted to the ovum by a force we do not yet understand, bursts through the zona radiata, loses its tail, its head enlarges, and forms the **male pronucleus**. The male and female pronuclei unite, and from their union springs the nucleus of the fertilized ovum. This is the centre from which all future developmental changes start. In the pronuclei, it will be remembered that the chromosomes were reduced to half the usual number; by their union the full complement of twenty-four is again restored in the fertilized

¹ In the sheath of the middle piece is also included an element scattered through the substance of the cell body of the parent germinal cell—the element known as mitochondria or chondriosomes (see J. Duesberg, *Biol. Bulletin*, 1919, vol. 36, p. 71; E. V. Cowdry, *Contributions to Embryology*, 1918, vol. 8, p. 41).

² For literature on fate of spermatozoa in the uterus see J. H. F. Kohlbrugge, *Roux's Archives*, 1912, vol. 35, p. 1.

ovum. By the process of fertilization the characters of two human individuals are mingled. The mixed chromosomes of the nucleus of a fertilized ovum are laden with an assortment of the virtues and vices of both father and mother in a latent form. They transmit the characters of the race from one generation to another. The ovum may be, but rarely is, fertilized in the ovary, or between the ovary and ostium abdominale, the result being a pelvic gestation. The length of time the fertilized ovum takes to reach the uterus is not known exactly, but probably it spends from four to five days within the Fallopian tube. The musculature of the tube, as well as the action of the cilia, assist the fertilized and developing ovum in its progress to the cavity of the uterus.

Formation of the Embryo.¹—We are now to follow, step upon step, the changes which are to transform the fertilized ovum into a human embryo. With the fusion of the male with the female pronucleus the ovum begins to divide, thus giving rise to the first brood of cells, two in number ;

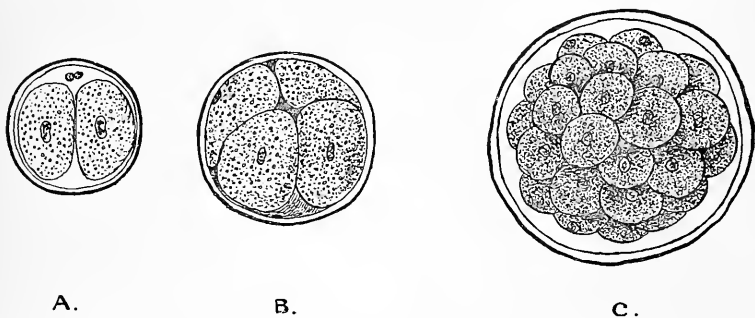


FIG. 12.—Showing the production of the Blastula or Morula from the Ovum. The oolemma (zona radiata or egg-membrane) persists up to the morula stage, even later.

A. The Ovum after the first division. B. After the second. C. The Blastula stage.

these in turn give rise to a second brood, four in number, and so on through successive stages, until a minute mass of cells replaces the ovum (Figs. 12 and 13) and thus a **blastula** or morula is formed—the first stage in the production of an embryo.

The production of the blastula takes place as the egg passes towards the cavity of the uterus, but before it has come into actual contact with the prepared lining membrane or decidua, it has entered a second and very important stage. A space or cavity appears within the blastula (Fig. 14) so that its cells become arranged in a definite manner. The cells which are going to give rise to the structures by which the embryo is to be nourished become arranged around the central cavity as a covering layer, while the cells which are to build up the embryo are enclosed within the covering layer (Fig. 14). In this manner the **blastocyst** is produced. At this stage, when the developing ovum is probably only half a millimetre in diameter ($\frac{1}{50}$ inch), it reaches the uterus. Its enveloping layer or **trophoblast** comes in contact with the decidua. In the blastocyst we

¹ For literature on early stages in the formation of the mammalian blastula see J. P. Hill, *Quart. Journ. Mic. Sc.* 1911, vol. 56, p. 1 ; 1918, vol. 63, p. 91.

recognize an embryogenic and a vegetative or yolk pole (Figs. 13 and 14). In Vertebrates with huge stores of yolk in their ova, such as birds have, the vesicle is filled by yolk-bearing cells, continuous with the enveloping layer at the *vegetative pole*, opposite to the inner cell mass.

We now pass on to a further or third stage, concerning which our knowledge is as yet imperfect. By virtue of the phagocytic power of its outer or trophoblastic layer, the blastocyst embeds itself in the decidual membrane of the uterus towards the end of the first week of development. In its earlier stages all developmental efforts are concentrated on the growth of the outer or trophoblastic layer which is to provide the embryo with nourishment; hence the rapid expansion of the blastocyst and the multi-

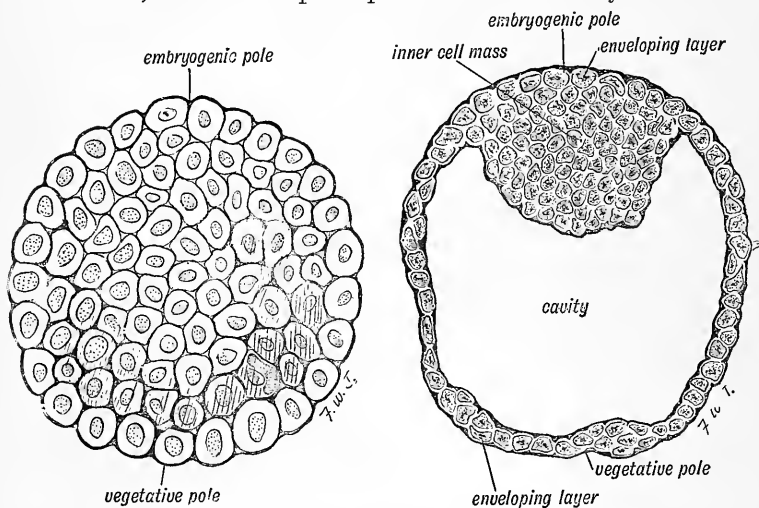


FIG. 13.—Stage I. The Blastula.

FIG. 14.—Stage II. The Blastocyst. (After Van Beneden.)

plication and spread of the trophoblastic cells. Early in the second week a vesicular structure, measuring little more than a millimetre in diameter, has been produced (Fig. 15). The inner cell-mass shown in Fig. 14 has now become differentiated into three sets or systems (Fig. 15): (1) a hypoblastic or **entodermal** set, grouped so as to form the wall of a minute vesicle—the fore shadow of the alimentary or archenteric system of the embryo; (2) an epiblastic or **ectodermal** set, enclosing another minute fluid space—the cavity of the **Amnion**. We shall see that the ectodermal cells in the floor of this cavity, the side abutting on the archenteric vesicle, will go to the formation of the embryo, while the cells of the side and roof will form merely the lining of the amniotic cavity, within which the embryo will become developed; (3) a third system—the mesoblastic or **mesodermal**—of cells has made a precocious appearance, surrounding the archenteric and mesodermic vesicles, lining the inner surface of the trophoblast and filling the space between the vesicles—the trophoblastic wall—with exceedingly fine fibrils (Fig. 15). These mesodermal cells are heralds of the great system out of which are to arise the blood and the vessels, muscle,

bone, ligaments and all the connective tissue structures of the body. Thus in the second week, embedded within the decidua, the developing human blastocyst reaches a third stage—one in which the embryo is represented by two vesicular structures—the **biventricular blastocyst**. The youngest human embryo of which we have accurate knowledge represents the terminal phase of this stage of development. This embryo was investigated and described by Teacher and Bryce in 1908.¹ The inner vesicles are still excessively small, the amniotic measuring only .15 mm. in diameter, while the archenteric is still less. On the other hand, the containing or trophoblastic vesicle is relatively large, measuring almost 2 mm. in its longest diameter and the trophoblastic cells are pressing outwards into the decidua by a process of most active growth. It is estimated that the Teacher and Bryce blastocyst is at the end of the

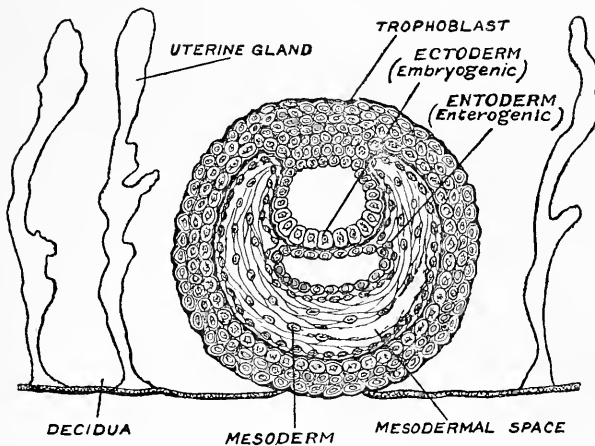


FIG. 15.—The Blastodermic Stage.

second week of development. Towards the end of the second week or commencement of the third a very important change, reproduced in Fig. 16, carries the blastocyst on to a further or *fourth stage* of development. The **coelomic cavity** or space, the primitive representative of the peritoneal, pleural and pericardial cavities is produced by the cleavage or separation of the mesoderm into two layers. One layer—the inner—covers the archenteron, its wall being now made up of two strata—an inner of entoderm and an outer of mesoblast or mesoderm; this double-layered wall is known as the **splanchnopleure**. The other layer of mesoderm—the outer, covers the outer surface of the amniotic cavity (Fig. 16) and the inner aspect of the trophoblastic wall. We shall see that the double-layered amniotic wall really represents the wall which encloses the abdominal and thoracic cavities; the double stratum made up of epiblast or ectoderm

¹ For literature on very early human embryos see T. H. Bryce and J. H. Teacher, *Contributions to the Study of the Early Development and Embedding of the Human Ovum*, Glasgow, 1908; the more recent literature and data are given by Dr. Geo. L. Streeter, *Contributions to Embryology*, 1920, vol. 9, p. 389.

and mesoderm or mesoblast is known as the **somatopleure**. The addition of mesoderm to all of these epithelial walls endows them with the power of forming blood vessels and blood. So far the growing blastocyst has depended for its sustenance on what the trophoblastic layer could absorb from the decidua but with the addition of mesoderm to the trophoblastic layer we have the outer or enveloping layer endowed with new and important properties. We shall see that the mesoderm on the archenteron and also that which lines the trophoblastic wall are the first to produce blood vessels and blood. With the addition of mesoderm to the trophoblastic wall we apply a new name to the outer or enveloping wall—namely the **chorion**. Through the chorion the embryo is to draw its oxygen and

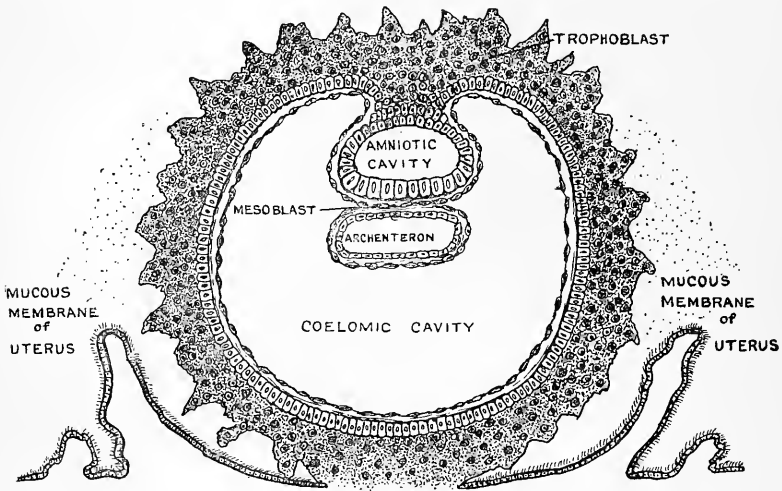


FIG. 16.—Showing the Origin of the Primitive Coelom, the Mesoblast and Cavity of the Amnion during the Development of the Human Ovum. (After T. H. Bryce.)

nourishment from the mother and get rid of its carbon dioxide and waste products.

In 1899 Dr. Peters gave a full and clear description of an embryo at this stage of development. The whole blastocyst was as yet of small size—only 1.6 mm. ($\frac{1}{16}$ inch) on its longest diameter (Fig. 17). The enveloping epiblast and its lining of mesoblast now form a distinct but non-vascular chorion. The archenteric vesicle is still of minute dimensions (Fig. 17). The amniotic cavity, formed within the enclosed ectoderm is larger, and the cells lining it have become differentiated into two kinds (Fig. 17). An area of columnar cells, forming the floor plate of the cavity, produces ultimately the epithelial covering of the body, and all the cells and fibres of the nervous system. The flatter cells which line the dome of the cavity will form the epithelial lining of the Amnion; the outer layer of mesoderm affords a covering to the amniotic ectoderm (Fig. 17). Fluid collects within the cavity of the amnion; floating in the fluid, the human embryo will develop. Thus the delicate embryonic tissues, being equally supported

on all sides by the amniotic fluid, may pursue their developmental courses, unhindered by the influence of gravity, and uninjured by the pressure, to which the uterus within the abdomen is subjected by the movements of respiration or bending of the trunk. If the fluid is deficient or absent then many forms of malformation may result.

It is in this stage (Stage IV.) that it becomes possible to detect the foundation or *Anlage* of the embryo. It is represented by the plate or lamina of tissues which separates the cavity of the archenteron from the cavity of the amnion (Fig. 17). The growth of the embryo remains in abeyance ;

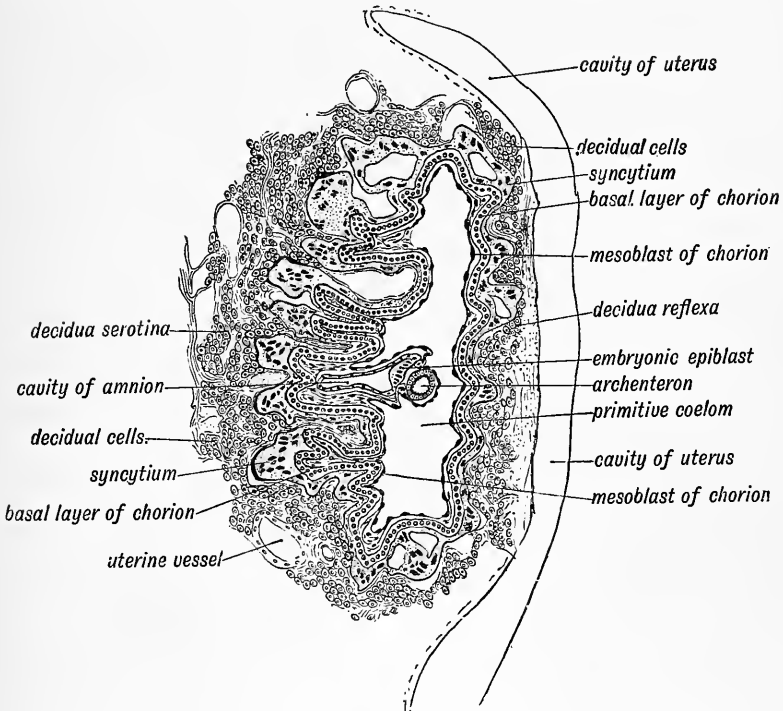


FIG. 17.—Stage IV. Section through the bivesicular blastocyst embedded in the wall of the Uterus. (Modified by F. W. Jones from figures given by Peters and Selenka.)

all the developmental energy is thrown into the upbuilding and expansion of the enveloping epiblast or **Trophoblast** as Hubrecht named it in 1889, for he recognized that its chief function was to provide the embryo with the means of nourishment (*τροφός*, a feeder). Thus in the earlier stages of development the actual embryo remains in abeyance, while the tissues which protect it and nourish it grow and develop with exceeding rapidity. Already, in Stage IV., it is seen that the epithelium forming the trophoblast has become differentiated into (a) a **Basal Layer** (Langhan's cells), (b) masses of cells, which have undergone multiplication without separation ; this formation is known as **Syncytium** (Fig. 17). The syncytium is chiefly developed on that aspect of the developing ovum which is directly in contact

with the wall of the uterus. It is remarkable not only for the imperfect separation of its cells, due probably to the rapidity of its growth, but also for the extraordinary phagocytic power it exercises on the mucous membrane of the uterus. Processes of the syncytium burrow within the thickened and vascular mucous membrane in a systematic and regulated manner; they absorb the tissue with which they come in contact, and lay open blood vessels of the mucous membrane. The maternal blood escapes into spaces enclosed by the syncytial processes or into lacunae formed by the vacuolation of processes. In certain circumstances syncytial cells escape into the general circulation and form malignant growths. If the developing ovum be arrested in the Fallopian tube the syncytium, owing to the extreme

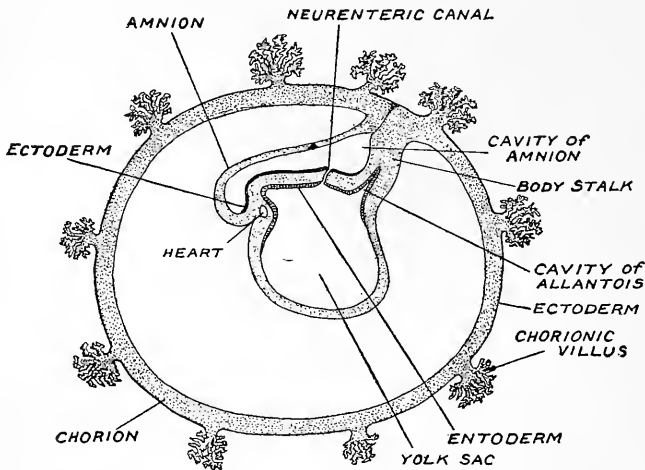


FIG. 18.—Stage V. Diagrammatic Section of a human pregnancy towards the end of the 3rd week of development, showing its demarcation into embryo and membranes. (After Graf Spee.)

thinness of the lining membrane, quickly eats its way into and through the wall of the tube.

In Fig. 18 there is given, in a diagrammatic form, the stage of development reached about the end of the third week. A very rapid growth sets in during this week; the chorionic vesicle which at Stage IV. measured only 2 mm. in its longest diameter, has become five times that length—an object easily visible to the naked eye. Villi grow out from it, at first simple and then branched; blood spaces filled by maternal blood are formed between the villi. In the villi, blood vessels and blood are being formed but a circulation is not yet established. The embryo is now definitely represented by a plate or shield—the **embryonic plate**, composed of three layers of tissues—an upper or ectodermal derived from the floor of the amniotic vesicle; a lower or endodermal formed by the roof of the archenteric vesicle and an intermediate formed by mesoderm or mesoblast. On the upper surface of the flat embryonic plate, which has a total length of about 1.5 mm., appears on its hinder or caudal half, the **primitive streak**; at the anterior end of the streak a perforation is formed—the **neurenteric**

canal which places the amniotic cavity in communication with the archenteric vesicle (Fig. 18). The nature of the primitive streak and of the neur-enteric canal we shall discuss later (see p. 38). The archenteric vesicle has also undergone a rapid growth, now measuring 2 mm. in diameter and we can recognize in it (see Fig. 18) the beginning of a division into two parts, the **yolk sac**—which contains a stock of nourishment and will come to lie outside the embryo and a part which remains applied to the embryonic plate and will form the alimentary canal system. The part which will come to lie within the embryo already shows a division into three parts—a forward diverticulum—the rudiment of the **foregut**, a posterior diverticulum—the rudiment of the **hind gut** and an outgrowth from the

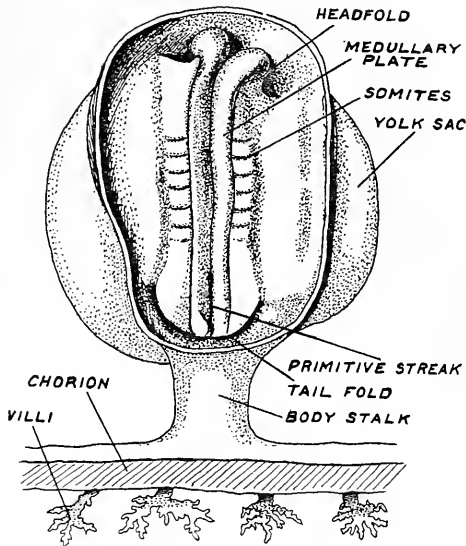


FIG. 19.—The formation of the medullary folds and somites on the embryonic plate.
From Prof. Pfannenstiel's model of an embryo measuring 1.95 mm. in length.

hind gut—which represents the structure known as the **allantois**. The embryonic plate, with the amniotic and archenteric vesicles, is bound to the chorion by the **body-stalk** (Fig. 18)—the rudiment of the umbilical cord. Thus towards the close of the third week human pregnancy is represented by (1) an embryonic plate, (2) a yolk sac, (3) amnion, (4) body-stalk, (5) chorion.¹

We shall now concentrate our attention on the growth of the embryo which from the end of the third week to the end of the fifth undergoes a very rapid transformation. The changes to be described follow very rapidly and constitute a **sixth stage**. About the end of the third week two folds—the **medullary folds**—begin to rise up along the head end of the

¹ For recent literature on embryos at Stage V. see Geo. L. Streeter, *Contributions to Embryology*, 1920, vol. 9, p. 389; N. W. Ingalls, ditto, 1918, vol. 7, p. 111; H. Triepel, *Anat. Hefte*, 1916, vol. 54, p. 149.

embryonic plate (Fig. 19), thus enclosing the neural plates from which the brain and spinal cord are to be developed. The rising up of the medullary folds is accompanied by the appearance of another very important developmental process—the cleavage or **segmentation** of the mesoderm on each side of the medullary folds into segments or somites. Segmentation commences in the posterior region of the head and spreads backwards. Thus the head region of the embryo is the first to be differentiated and we have every reason to suppose that the segments at the cranial end are the oldest in an evolutionary sense. With the appearance of somites the human embryo manifests its vertebrate character.

The human embryo reconstructed from serial sections by Professor Thompson in 1907 shows the great advance made during the fourth week¹

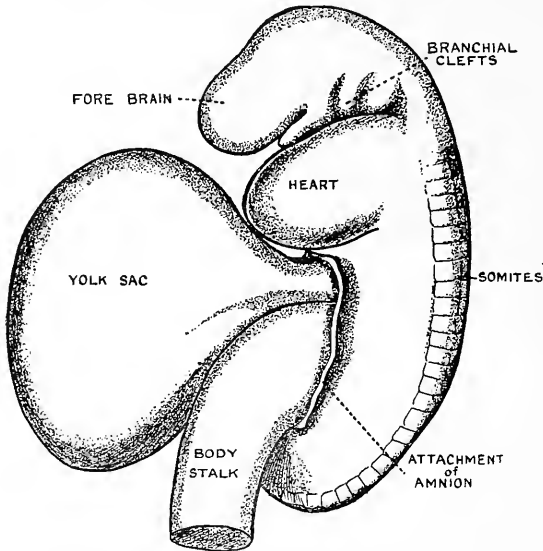


FIG. 20.—Human Embryo 2.5 mm. long, towards the end of the fourth week of development. (Professor Peter Thompson.)

(Fig. 20). The medullary folds have fused along their crests and enclosed the neural plates to form a canal or tube, the process of segmentation is spreading rapidly backwards, the head and gill arches can now be recognized and although the embryo measures as yet less than 3 mm. in length, the main parts of the adult body, saving the limbs, are clearly foreshadowed.

We have reached what may be termed a seventh stage in the development of the human embryo. We must now turn to some of the chief internal changes which have been taking place, and this can best be done by

¹ For description of embryos in the 4th week of development, and for references to other descriptions see P. Thompson, *Journ. Anat. and Physiol.* 1907, vol. 41, p. 159; F. Wood Jones, *Proc. Anat. Soc. Grt. Brit.* June, 1903; A. Low, *Journ. Anat. and Physiol.* 1908, vol. 42, p. 237; W. E. Dandy, *Amer. Journ. Anat.* 1910, vol. 10, p. 85; Sussana P. Gage, *Amer. Journ. Anat.* 1905, vol. 4, p. 409. For the most recent descriptions: see Prof. D. Waterston, *Journ. of Anat.* 1915, vol. 49, p. 92; J. Crawford Watt, *Contributions to Embryology*, 1915, vol. 2, p. 5.

comparing sections across the flat embryonic plate of a pregnancy in the third week of development (Stage V.) with a section of one such as made by Professor Thompson which has reached Stage VII. (see Fig. 21, *A, B*). When such sections are compared the following changes will be noted : (1) A narrow plate of modified ectoderm or epiblast, stretching along what will be the median dorsal line of the body, becomes depressed, thus forming the floor of a groove ; the lateral margins of the groove rise up, meet together and fuse along the middle line. Out of the **neural tube** thus enclosed are developed the brain and spinal cord. (2) In a somewhat similar manner a strip of cells along the median dorsal wall of the archenteron is separated as a tube to form the **notochord** (Fig. 21, *A, B*). Round the notochord are developed the spinal column and the greater part of the base of the skull. (3) Indications are to be seen of a separation of the

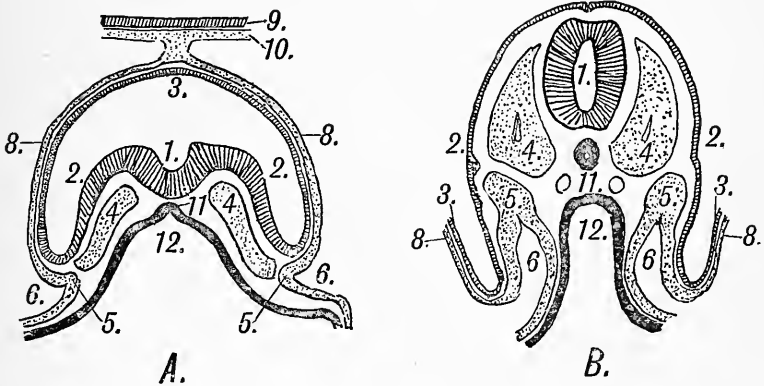


FIG. 21.—Schematic Transverse Sections of two Human Embryos.

A, In the 3rd week of development. *B*, In the 4th week of development.

The numbers are placed on corresponding points: Epiblast, shaded; hypoblast, black; mesoblast, stippled.

- | | |
|---|---|
| 1. Neural groove and canal. | 6. Coelom, bounded by the somatopleure externally and splanchnopleure internally. |
| 2. Epiblast of embryo. | 8. Mesoblast on amnion. |
| 3. Epiblast lining amnion. Only the attachment of the amnion is represented in <i>B</i> . | 9, 10. Chorion. |
| 4. Paraxial mesoblast. | 11. Notochord. |
| 5. Intermediate cell mass. | 12. Archenteron. |

archenteron into an intra-embryonic part, which will form the **alimentary tract**, and an extra-embryonic part, which becomes the **yolk sac**. (4) The mesoderm on each side of the embryo shows a division into four parts : (a) **paraxial mesoderm** (4, Fig. 21) from which the voluntary musculature, as well as other parts of the body system arise ; (b) **intermediate cell mass** (5, Fig. 21), in which the renal and genital organs are developed ; (c) somatic mesoderm, this layer with the **ectoderm** over it forms the **somatopleure**, the outer wall of the coelom ; from the coelom are developed the pericardium, pleura and peritoneum ; (d) the splanchnic mesoderm, which covers the intestine and yolk sac ; the splanchnic mesoderm and entoderm together form the **splanchnopleure**. (5) Indications can be seen of the division of the coelom into intra- and extra-embryonic parts (6, Fig. 21).

When the umbilicus contracts and closes, these two parts of the coelom are finally separated. It is also during the fourth week that the paraxial mesoderm becomes separated into primitive segments, or **somites**, formerly known as protovertebrae. In the embryo shown in Fig. 20 twenty-three pairs are already separated.

In Fig. 22 is represented the fully differentiated human embryo—a stage of development—which we may call the **eighth stage**, reached about the end of the fifth week.

From crown to rump the embryo about this time measures 5 mm.—one-fifth of an inch. The buds of the upper and lower extremities have now appeared; segmentation has reached almost to the tip of the tail, there being three occipital and 35 body somites, the last representing the sixth coccygeal or caudal. The mouth is becoming apparent; so are the eye and nose; the gill arches, four of which are apparent in the neck, have reached

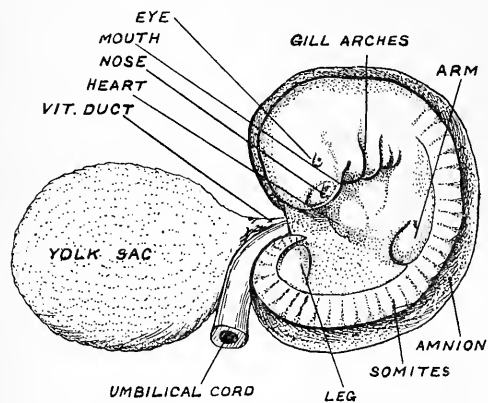


FIG. 22.—Showing a human embryo, 5 mm. in length, at the end of the 5th week of development. (After Keibel and Mall.)

their highest development; a blood circulation is now fully established, the body stalk having been transformed into the umbilical cord. The yolk sac is now joined to the embryonic gut by a long narrow duct—the vitello-intestinal duct (Fig. 22).

Origin of Ova and Spermatozoa.—Towards the end of the stage just described, the **genital ridges** arise from the intermediate cell mass and project into the coelom, one at each side of the root of the mesentery (Fig. 23). The mesothelial cells which line the coelom assume a columnar form at the root of the mesentery and over the genital ridges; between these cells appear **primitive germ-cells** (primordial ova) characterized by their large size and reaction to certain stains. Hitherto it has been assumed that the germ-cells arose from the mesothelial columnar cells which cover the ridge. Beard, during a prolonged and accurate investigation of the development of fishes, especially of the skate, discovered that the germinal cells were not formed in the genital ridges but appeared at a very early stage corresponding to that described here as Stage I. When the coelom is formed they migrate towards the genital ridges. There is nothing strange in such a migration for it is a daily occurrence in the adult body for leucocytes to be drawn in crowds to a site of infection by an obscure force which is named *chemotactic*. It is, then, far from unlikely that the primitive germ-cells are separated at an early stage in the division of the ovum and then subsequently seek a nidus in the genital ridge. We shall see that nerve cells migrate under similar influences. We may

suspect that the germ-cells which fail to reach the suitable nidus, which the genital ridges afford, are absorbed, or, as Beard has suggested, they may give rise to those curious tumours known as teratomata. The manner in which the primitive germ-cells are carried within the genital ridge by tubular incursions of the mesothelium covering the ridge has been already described, but we are ignorant of the circumstances which determine the production of spermatozoa and a testicle in one individual, and the formation of ova and an ovary in another. It is not until the embryo has attained a length of 15 mm. in the seventh week of development that it is possible to distinguish testicle from ovary.

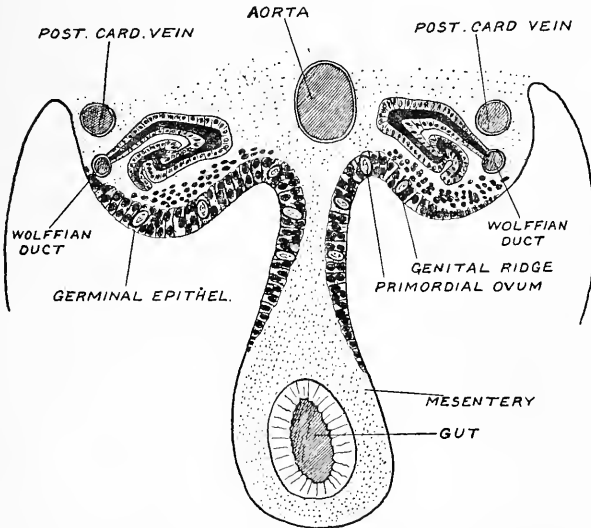


FIG. 23.—Diagrammatic Section of the roof of the Coelomic cavity of a human embryo in the fifth week of development, showing the position of the Genital Ridges in which the Ovary or Testicle is formed.

Thus in the space of five weeks the cycle which produces new human seed from the old is accomplished and all the parts of a new human body are laid down in outline. In these five weeks the fertilized ovum has given rise to (1) germ-cells which are endowed with the combined properties of the ovum and spermatozoon from which they were produced; (2) an embryo in which these cells are nourished and protected; (3) membranes by which the embryo is protected and nourished during intrauterine life.

Having thus followed the chief developmental changes of the ovum, and seen how the embryo, the membranes and the reproductive cells are differentiated, we shall review in the next chapter the manner in which the ovum establishes itself in the cavity of the uterus and, for the space of nine months, passes a parasitic life there.

CHAPTER II.

THE MANNER IN WHICH A CONNECTION IS ESTABLISHED BETWEEN THE FOETUS AND UTERUS.

The Decidua.¹—Every menstrual period, the mucous membrane which lines the cavity of the uterus becomes hypertrophied and its vessels congested. If the ovum be not fertilized, then the surface layer of the mucous membrane dies and is cast off, but if fertilization occur then the process of hypertrophy proceeds and the mucous membrane now receives the name of decidua. The formation of the decidua is characterized by (1) the production of **decidual cells**—cells with a more or less rounded outline, large cell-body and relatively small nucleus—from the connective tissue cells which lie beneath the epithelial lining of the mucous membrane and between the tubular glands embedded in the mucous membrane (Fig. 17, p. 15); (2) the epithelial lining proliferates, the surface of the mucous membrane becoming rugose with pits and depressions; (3) the uterine glands become elongated and branched; ¹ their mouths are closed by the growth of the decidual cells; their fundi, abutting against the muscular coat, undergo no change; the elongated bodies of the tubes, between their mouths and fundi form cavernous spaces; (4) the vessels of the uterus increase in size and the capillaries of its mucous membrane are dilated. In this manner the uterus is prepared to receive the fertilized ovum. It is highly probable that these changes are influenced by an ovarian secretion, for, when the ovaries are removed, these changes soon cease to occur. The internal secretion of the corpus luteum exercises a stimulant action on the uterine tissues.

Implantation of the Ovum.²—When the fertilized ovum reaches the cavity of the uterus it has already attained the blastocyst form (Fig. 14, p. 12). The inner cell mass, from which the embryo will arise, projects within the cavity and is protected by the enveloping layer or trophoblast of the blastocyst, the whole ovum measuring about .5 mm. in diameter. Implantation occurs in one of the pits of the mucous membrane usually on the posterior wall of the cavity near the fundus of the uterus, but it may occur anywhere, that form being especially dangerous in which implantation occurs in the neighbourhood of the internal mouth of the uterus. The area of the trophoblast in contact with the uterine pit grows

¹ See Baumgartner, *Amer. Journ. Anat.* 1920, vol. 27, p. 203.

² See references, p. 13.

rapidly and throws off proliferating masses of **syncytium** (Fig. 17, p. 15) which burrow into the decidua, thus embedding and anchoring the blastocyst and by the absorption of the decidual tissue, providing nourishment for it. The blastocyst is peculiar in man and the anthropoids in that it becomes completely buried in the decidua. The parts of the decidua are thus distinguished : (1) the **decidua serotina** or **basalis**, the part to which the ovum became attached and into which the processes of syncytium grow (Figs. 17 and 24) ; (2) the **decidua capsularis** or **reflexa**, the part which covers the ovum and is stretched as the ovum grows ; (3) the **decidua vera**, which lines the rest of the uterus. The decidua vera ends at the internal os, the canal of the cervix producing no true decidual layer.

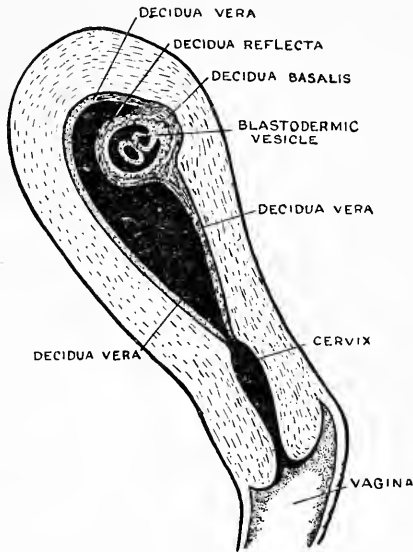


FIG. 24.—Section of the Uterus showing in a diagrammatic manner the Embedded Ovum and the differentiation of the Decidua into Three Parts.

With the growth of the embryo the decidua reflexa is brought in contact with the decidua vera. By the fifth month they have fused together, become flattened and partially atrophied. The decidua serotina, on the other hand, forms the basis in which the placenta is developed.

Nourishment of the Early Ovum.¹—The ova of birds and reptiles are laden with yolk and on this the developing embryo lives—the yolk being absorbed by the entodermal cells lining the archenteron. Primitive forms of mammals, such as the Duckbill and Echidna, have also large supplies of yolk in their ova, but in all other mammals the ova contain only a small supply of yolk ; hence the developing ovum has to draw its nourishment from the uterus. The secretion of the uterine glands contains a proteid (Emrys Roberts) which probably affords nourishment to the

¹ E. Emrys Roberts, *Journ. Anat. and Physiol.* 1910, vol. 44, p. 192 (Embedding of Ovum and Nutrition—Guinea-pig) ; Emrys Roberts, *Proc. Roy. Soc.* May 21, 1908.

ovum. The decidual cells contain vacuoles of fat and glycogen (J. W. Jenkinson) and these cells and their contents are absorbed by the trophoblast and passed on to the growing tissue.

Evolution of the Foetal Membranes.—In the first chapter we have seen that, almost from the beginning of development the embryogenic mass of cells is enclosed within a vesicle formed of trophoblastic cells. With the addition of a mesodermal tissue the trophoblastic vesicle becomes the **chorion**, the most important of the membranes which envelop the foetus; it comes soon to serve the foetus as lungs, stomach and kidneys. We have also seen the origin of the amniotic cavity and its surrounding membrane, the **amnion**; we saw, too, how the **yolk sac** arose from the primitive gut cavity or archenteron, and also how a diverticulum, known as the **Allantois**, arose from the hinder end of the archenteron. They all appear so simply and in so regular a sequence that we are apt to forget, from an evolutionary point of view, that they are relatively of recent origin. We can only understand their true nature by an appeal to comparative anatomy. The structures just named are not found in the lower vertebrates—amphibians and fishes, only in the higher—reptiles, birds and mammals; yet we are certain that the higher were evolved from the lower and that therefore these structures were evolved during the early history of the higher vertebrates. We can see that such a highly evolved structure as the human body is at birth could not have come into existence unless provision had been made for maintaining the individual during the months of embryonic and foetal life. Nature evidently accomplished this miracle without calling into being any new kind of structure; the chorion, amnion, allantois and yolk sac of higher vertebrates were produced from structures already in existence in their lower vertebrate ancestors. The yolk sac, we shall see, is part of the bowel which has undergone an exaggerated and precocious development and is cut off from the rest of the bowel and cast away by a species of natural surgery, when it has served its purpose in the upbuilding of the embryo. The allantois has been evolved by a precocious development and overgrowth of the apical portion of the primitive bladder; when this apical part has served its foetal purpose it too is sacrificed and the site of its separation closed. More marvellous still is the origin of amnion and chorion; they represent parts of the ventral body wall which have been so hurried forwards in point of time of development that they are actually produced in the human blastocyst before the main part of the embryonic body has commenced to form. The membranes which envelop the foetus—the amnion and chorion—are precocious overgrowths of a part of the body wall which is removed at birth, the umbilicus representing the scar which marks the site of amputation.

The Yolk Sac.—The most ancient method of providing for the growth of the embryo is by loading the ovum with yolk or *vitellus*. Everyone is familiar with the embryonic provision stored within a fowl's egg; in birds and reptiles the vitelline system reaches its highest development. The meal or yolk is already in the egg before there is an embryonic stomach to digest, absorb and serve it up as nourishment to the growing embryonic

structures. Hence one of the earliest efforts in the developing chick is to throw a containing wall—the archenteron—round the yolk. Even in the human embryo the yolk sac plays a very important part in the up-building of the body. In Fig. 25 is shown, in a somewhat diagrammatic form, the yolk sac of a human embryo at the end of the third week of

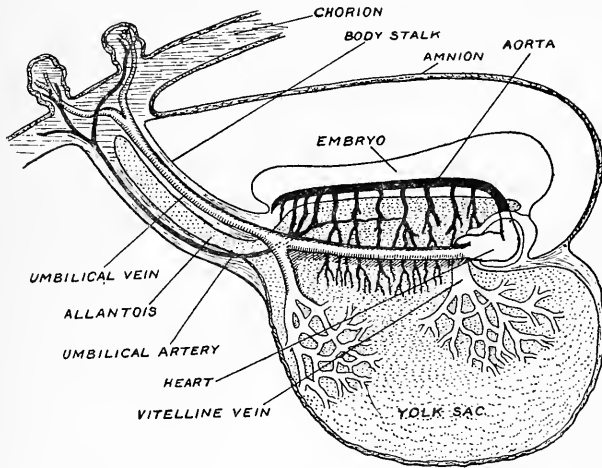


FIG. 25.—The Yolk Sac and early vessels of the human embryo about the end of the 3rd week of development. (Modified from Eternod.)

development when the yolk sac measures 2 mm. in its longest diameter and is at its point of maximum importance. A circulation has not yet been established, but blood vessels and blood islands are being rapidly formed in the mesodermal or mesenchymal tissues covering its entodermal lining (Fig. 26). The aortae—right and left—are being laid down and numerous communications are being opened up between the aortae and

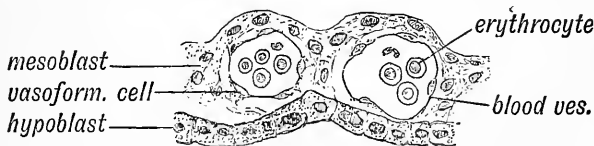


FIG. 26.—Section across the wall of the Yolk Sac, showing blood vessels and nucleated red blood corpuscles forming in its mesoblastic layer. (After Selenka.)

the vascular-plexus system of the yolk-sac and also between the yolk-sac system and the venous end of the cardiac tube where the vitelline veins are forming. We see all the parts being prepared for the establishment of a vitelline circulatory system. By the end of the fifth week of development the yolk-sac lies outside the body of the embryo (Fig. 22, p. 20) and is now joined to the bowel by a narrow canal—the **vitello-intestinal duct**. Very soon after this, the duct closes and atrophies, but the sac itself continues to grow until it reaches a diameter of 4 or 5 mm. Its further history we shall examine later (p. 88), but here we may state that when the umbilical

cord is fashioned the remains of the vitello-intestinal duct are enclosed within it, while the sac itself will be found at or near the placental end of the cord. In Fig. 26 is shown a section across a small part of the wall of the yolk sac to illustrate the manner in which embryonic blood corpuscles (erythrocytes) and blood vessels are formed in the mesodermal or mesoblastic stratum of its wall. The lining entoderm or hypoblast also gives rise to glandular structures.

The Allantois.—The allantois appears during the third week of development of the human embryo as an outgrowth from the hinder end of the archenteron or primitive gut cavity. To understand its true nature we must examine the structures in the lower vertebrates from which the allantois has been evolved. These parts are represented in Fig. 27—depicting a condition found in **amphibia**. The rectum and also the ducts of the testes—the two Wolffian ducts—end in a terminal passage—the cloaca. An expansion or diverticulum of the cloaca has been established as a receptaculum for urine—the bladder. The blood supply is peculiar.

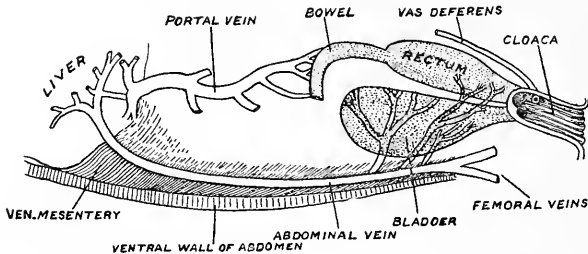


FIG. 27.—The cloaca, bladder and abdominal vein of a frog.

A large vein passes along the inner aspect of the ventral wall of the belly, draining the blood from the bladder and from the ventral wall of the belly, as well as from the hind-limbs and ending with the vein from the bowels and stomach in the portal system of the liver. Originally this ventral abdominal vein is double, there being a right and left vein which convey the blood of the bladder and of the ventral wall—but not that of the limbs—the connection of the femoral veins is secondary—direct to the heart. The arteries which supply the bladder and ventral wall spring from the common iliac arteries—these latter vessels representing direct continuation of the right and left primitive aortae. If, then, the allantois represents a precocious outgrowth from the apical region of the bladder and the chorion and amnion enormous and premature expansions from the ventral belly wall, we expect that their arteries would arise from the hinder ends of the embryonic aortae and their veins pass forwards on the body wall to terminate at first in the heart and afterwards in the liver. That is exactly what we do find, as may be seen from a reference to Fig. 25.

To see the allantois in its complete form one must examine the developing chick embryo (Fig. 28). The young of animals which are developed within a shell, need a receptaculum for the secretion from their kidneys; for this reason alone one can understand the expansion of the embryonic bladder.

But even in the chick its use as a store place for urinary excretions has become of minor importance; the mesodermal tissue which clothes the bladder has become the most important element; it has grown exceedingly rich in vascular tissue. As the allantois expands in the developing chick its vascular surface becomes applied to the inner aspect of the chorion through which it can absorb oxygen and discharge carbon dioxide. The apical part of the bladder has thus become converted into a "foetal lung," but its vessels are those we have just noted in the ventral area of the frog; its arteries—the **umbilical arteries** appear to be direct continuations of the two aortae, and its veins—the **umbilical veins**, pass to the heart and afterwards to the liver, just as in the frog.

In the human embryo, as is the case in all developing primates, the cavity of the allantois is never represented by more than a tubular outgrowth into the body stalk (see Figs. 18 and 25) and even this degenerates very soon. The human embryo has no need for a bladder, as it can discharge its urinary excretion into the maternal circulation as soon as the

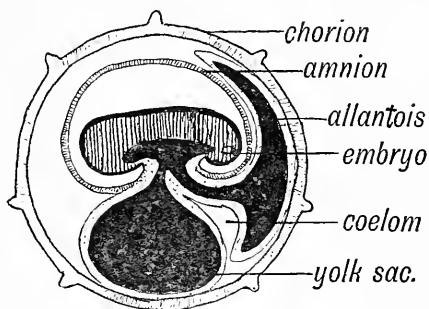


FIG. 28.—The primitive form of the Allantois. (After Turner.)

chorionic circulation is established. It is otherwise with the mesodermal covering of the allantois; we shall see that this element takes the chief part in the vascularization of the chorion. In Fig. 25 it will be seen that the umbilical vein is connected with the vascular system of the yolk sac at the root of the allantoic diverticulum. We may regard the allantoic circulation as an enormous expansion from the more primitive circulation of the archenteron.

The Evolution of the Amnion and Chorion.—If our knowledge were confined to the highly specialized processes which give rise to the amnion and chorion, the enveloping membranes of the human embryo, it would be almost impossible for us to guess that these structures represent, in reality, folds of the embryo's own belly wall. They come into existence before even the embryo itself is apparent. Their very humble but marvellous origin is illuminated when we examine the manner in which they arise in reptiles, birds and the lowest mammals. In Fig. 29, which represents diagrammatic sections across chick embryos, the origin of the enveloping membranes is set out in a pictorial form. The somatopleure or body wall is seen to arise as a fold at each side of the embryo and mounting upwards ultimately meet and fuse along the median dorsal line. The inner

fold separates from the outer and forms the amnion; the outer remains as a membrane enveloping the embryo, amnion, yolk sac and allantois and is the basis of the chorion—the prechorion it is named in the chick. From the diagrams one would infer that the greater part of the chick's body wall was folded off to form the enveloping membranes but when we remember that the yolk sac represents a premature but enormous development of a localized part of the bowel, we may justly conclude that the enveloping part of the somatopleure represents a limited area of the ventral part of the abdominal wall—the part drained by the ventral abdominal vein, which has become greatly expanded. The assignation of part of the somatopleure to form the enveloping membranes involves no

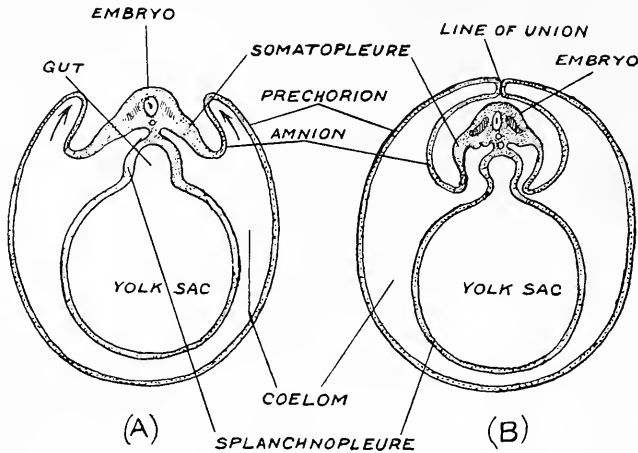


FIG. 29.—Illustrating the manner in which the chorion and amnion arise in the chick embryo from folds of the somatopleure—the body wall of the embryo. In *A*, the folds are seen in the act of growing upwards to cover the embryo; on *B*, they have met over the embryo.

sacrifice of muscle or nerve in the belly wall of the embryo; we shall see that these elements invade the somatopleure long after the membranes have separated. Only two elements of the belly wall have been utilized in the formation of the amnion and chorion: (1) the epithelial or ectodermal covering of the skin which takes on a phagocytic action; (2) the mesodermal element which gives rise to connective tissue, blood vessels and blood cells. Prof. J. P. Hill¹ has demonstrated that in the developing marsupial ovum, when only three cell-divisions have occurred and only 16 or fewer cells are formed, those which are to give rise to the epithelial covering of the chorion and amnion can be distinguished from the smaller number which is to form the embryo. In the human ovum it is also so; we have seen that the epithelial covering of the chorion—the trophoblast—is the first structure to be differentiated in the development of the blastocyst. In early days primitive man required no scaffolding or machinery to build his rude hut; in great modern building extensive

¹ *Quart. Journ. Mic. Sc.* 1918, vol. 63, p. 91.

scaffolding and elaborate machines have to be erected before ever building has begun. The chorion and amnion are the scaffolding thrown up for the development of the higher vertebrates and they were evolved out of simple parts of the belly wall.

The amnion which contains a fluid in which the embryo floats and has its very delicate growing tissues equally supported on all sides, is not required in the development of fishes or amphibians; their eggs are hatched in water and the larvae live in water and have therefore no need of an amnion. This structure became necessary when the ancestry of the higher vertebrates took to a life on land. To allow their young to develop in the ancestral medium the amnion was evolved from a duplicature of the embryo's body wall. Having thus given a clue to the evolutionary history of these marvels of adaptation—the amnion and chorion—we return to note stages by which the placenta is produced from the chorion and a foetal circulation established.

Chorionic Villi.¹—The origin of the chorion from a combination of two elements—the trophoblast (enveloping layer of ectoderm) and an extension from the somatic mesoderm—has been already traced (p. 14). The division of the trophoblast into a basal layer and syncytium was also mentioned. As soon as the ovum is embedded in the decidua, processes of syncytium invade not only the serotinal but also the reflected or capsular part (Fig.

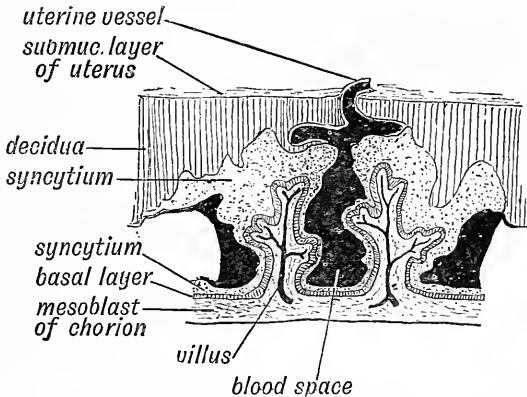


FIG. 30.—Diagrammatic Section of the Decidua Serotina (formed from the mucous membrane of uterus) and Chorion, to show the manner in which the placental blood spaces are formed.

17, p. 15). Villi, containing a core of mesoblast and a covering of the basal layer of chorionic epithelium, grow out into the syncytial masses (Fig. 30). The villi continue to divide and redivide thus becoming arborescent. During the third week the mesodermal tissue of the chorion,

¹ For details and literature relating to the formation of placental structures see A. C. F. Eternod, *L'œuf humain*, Geneva, 1909; A. Eternod, *Compt. Rend. Congrès internat. d'Anat.* 1905, p. 197; *Compt. Rend. Assoc. des Anatomistes*, 1909, p. 1; A. W. Hubrecht, *Anat. Anz.* 1905, vol. 31, No. 13 (Nature of trophoblast); J. W. Jenkinson, *Vertebrate Embryology, comprising the early history of the embryo and its foetal membranes*, 1913.

particularly of its villi, becomes the site of active formation of blood vessels, blood cells being developed within the vascular lumina. Similar formations are taking place in the body stalk, in the wall of the yolk sac and also in the embryo itself, so that by the end of the third week a tubular heart, dorsal aortae, vitelline and umbilical veins communicating with a great capillary network have been laid down (Fig. 25, p. 25). About the end of the third week or beginning of the fourth a circulation of blood has been established in the chorion. Direct prolongations of the two dorsal aortae now extend through the body-stalk to the chorion—these extensions forming the umbilical arteries (Young and Robinson). The umbilical veins carry the blood from the chorion through the body stalk to the embryonic heart. The chorionic circulation replaces functionally that of the yolk sac. Through the chorionic circulation the embryo is nourished.

Formation of Placental Blood Spaces.—The decidual nutriment only affords a temporary supply. In the last few years the researches of a number of German investigators, but especially of Peters and Selenka, have shown that the maternal circulation is placed at the disposal of the chorionic villi in a simple manner. The syncytium, as it burrows into and replaces the serotinal part of the decidua (Figs. 24, 30), invades the maternal blood vessels, and replaces their walls by its own tissue. The masses of syncytium between the main villi break down and thus form large spaces into which the decidual vessels, which were enclosed by the syncytium, freely open (Fig. 30). Through these spaces the maternal blood circulates, supplied by the uterine arteries and carried away by the uterine veins. The trophoblast contains a ferment which prevents coagulation of the blood in the intervillous spaces thus formed (Young). The extension of the syncytium, the formation of villi and of blood spaces, go on until the 5th month. By that time the basal and syncytial layers of epithelium on the villi are replaced by a single flattened layer of cells. The vascular villi of the chorion hang within the decidual blood spaces, and draw from the maternal blood oxygen and nutriment for the supply of the embryo. Processes and partitions derived from the syncytium remain to bind the chorion to the uterine wall.

Formation of the Umbilical Cord.—At the end of the third week of development (see Figs. 18, p. 16, 25, p. 25), when the embryo forms a cap on the yolk sac and a plate in the floor of the amniotic cavity, neither umbilicus nor umbilical cord are differentiated. The **body-stalk** unites the caudal end of the embryo to the inner wall of the chorion, and appears to represent a posterior extension of the embryonic body, but in reality it is formed out of a reflection of part of its ventral wall. It serves the purposes of an umbilical cord to the early embryo. A section across the body-stalk (Fig. 31) shows that two umbilical arteries, two umbilical veins, and the canal of the allantois lie in its mesoblastic basis, and while its upper epiblastic surface projects, like the rest of the embryo, within the cavity of the amnion, its lower surface lies in the wall of the extra-embryonic coelom, in contact with the yolk sac. The structures in the body-stalk are those which we find in the ventral belly-wall of the frog (Fig. 27).

To understand the origin of the umbilical cord one must observe closely the attachment of the amnion at this early stage. It is attached to the circumference of the embryo and body-stalk (Figs. 20 and 21); to the zone of somatopleure which unites the embryo and the amnion, the name of **junctional ring** may be given, with the clear understanding that the body-stalk enters into the formation of the posterior part of the ring. From the junctional ring the umbilical cord is developed. While the embryo grows rapidly and expands within the amnion the junctional ring retains its embryonic size (see Fig. 2). The parts of the yolk sac and coelom which are surrounded by the ring now appear to be constricted (Fig. 21). In the second month the junctional ring begins to elongate and form a cord-like structure, in which an umbilical and a placental extremity can be recognized (Fig. 32). The amnion is attached at its placental extremity.

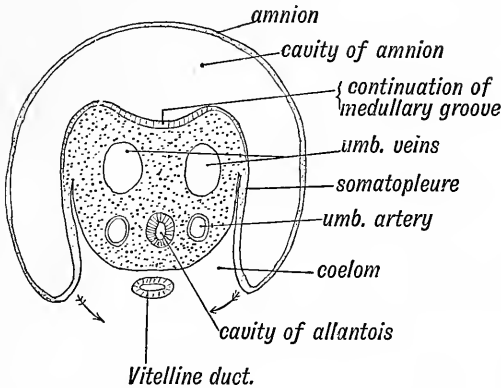


FIG. 31.—Section across the Body-Stalk. (His.)

The mesoderm of the junctional ring forms the jelly-like tissue (Wharton's jelly) of the umbilical cord in which are embedded the umbilical arteries and one umbilical vein, formed by the fusion of the right and left vein. By the third month the cord measures 12 cm.; and 40 cm. by the ninth month. The elongation of the junctional ring to form the cord necessarily affects all those structures which lie within the ring—the neck of the yolk sac (vitello-intestinal duct), the coelomic space or primitive peritoneal space, the cavity of the allantois. All of these are included within the cord, and are obliterated during its elongation. The coelomic or peritoneal space at the umbilical end of the cord closes in the third month, but it may remain open to birth and form the seat of a **congenital umbilical hernia**. As an exceptional occurrence, the intra-embryonic parts of the allantois or of the vitello-intestinal canal may remain patent as far as the umbilicus, and with the removal of the cord at birth give rise to a **urinary** or a **faecal fistula**.

Formation of the Placenta.—The condition of the membranes in the third month (Fig. 32) differs from that of the first month (Fig. 18) by the formation of the placenta. In the first month the chorion is uniformly covered by shaggy villi, this being the permanent condition in low primates (Lemurs). In man the chorionic villi which project within the decidua

serotina hypertrophy, while those within the decidua reflexa atrophy, and in this way the discoidal placenta of man is formed (Fig. 32). In lower primates (Monkeys) there are two discs (bi-discoidal), and this form occasionally occurs in man.

The elements entering into the formation of the placenta are diagrammatically shown in Fig. 33. They are :

1st. The decidua serotina, formed from the mucous membrane of the uterus. It is almost completely replaced by the syncytium and chorionic

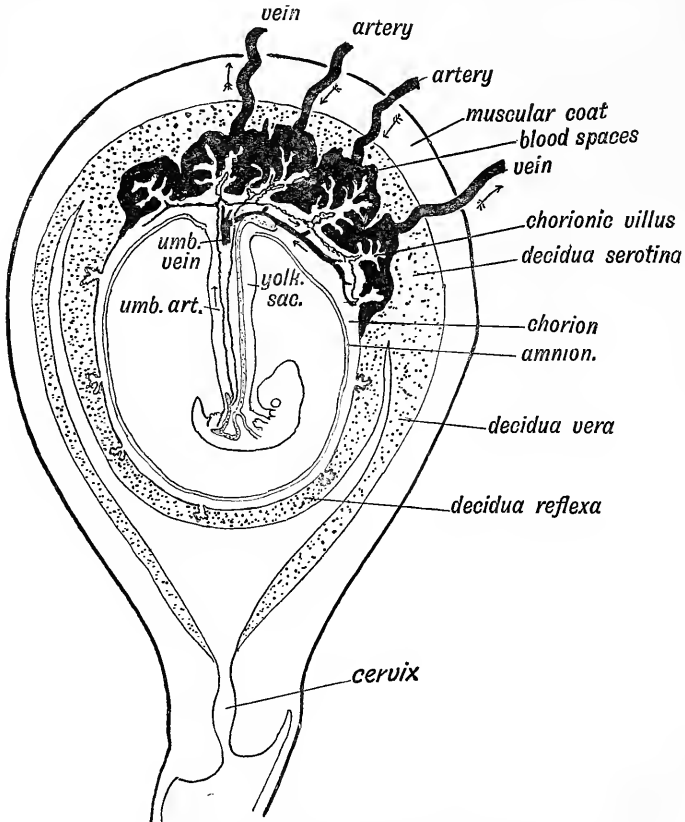


FIG. 32.—Showing the arrangement of the Amnion, Chorion, and Decidua in the 3rd month and the Formation of the Placenta.

villi. Only the basal layer remains to furnish a new lining to the uterus when the membranes and placenta are shed after the birth of the child.

2nd. The chorion, or, strictly, prechorion.

3rd. An allantoic element which is fused with the mesoderm of the chorion in the human ovum. In the human placenta it is impossible to distinguish the 2nd from the 3rd element ; both are fused in the mesoderm of the chorion from the beginning.

4th. The amnion, which becomes applied to the inner surface of the chorion, thereby obliterating the extra-embryonic coelom (Figs. 32, 33). Thus it will be seen that almost the entire placenta is produced from the ovum and is truly a part of the foetal structures. The decidua, the only maternal element, merely affords a nidus or suitable bed for the development of the foetal structures.

From the inner surface of the fully-formed placenta, the amnion, a thin transparent membrane, is easily stripped off. The outer or uterine surface of the placenta is rough and shaggy, being mainly composed of the greatly hypertrophied villi developed from the serotinal or attached area of the chorion. The villi are grouped in clumps or cotyledons, between which are fibrous strands and partitions, which pass through the whole thickness of the placenta and thus maintain its fixation to the uterus. The manner in which the trophoblast covering the villi becomes changed until it forms

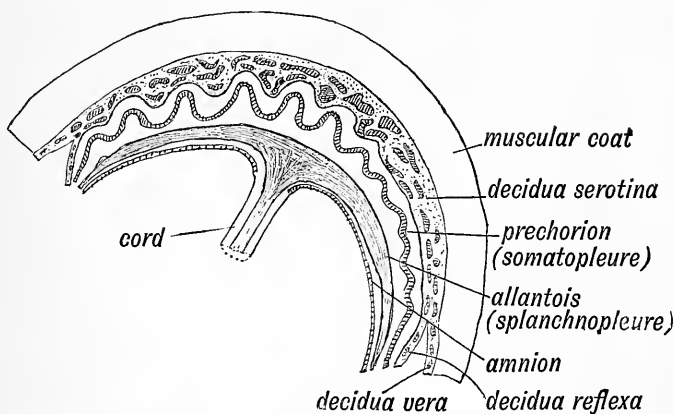


FIG. 33.—Diagrammatic Section to show the Elements which enter into the formation of the Placenta. The trophoblast on the outer side of the prechorion has been omitted for the sake of simplicity.

merely a thin epithelial covering has been already described (p. 29). Into the villi pass branches of the umbilical arteries, ultimately forming a fine capillary network, from which the arterialized blood is returned to the foetus by the umbilical veins. Everywhere the blood of the foetus is separated from that of the mother by a thin capillary wall and a layer of flat epithelial cells; through this wall exchanges between the foetal and maternal circulation take place. The villi project within great blood spaces formed in the decidua serotina (Fig. 32). The ovarian and uterine arteries end in these blood sinuses, and the ovarian and uterine veins begin in them.

At full term all the membranes of embryonic origin come away in the after-birth; also the decidua, except a thin, deep layer next the uterine muscle, which contains the deepest parts of the uterine glands. From this layer the mucous membrane of the uterus is regenerated.

The establishment of the developing ovum within the uterus of the mother constitutes one of the most marvellous chapters of Embryology.

It is apparent that in the evolution of the higher mammals the young have become modified to pass the first stage of life as uterine parasites. In this chapter we have seen that the ovum has already reached a considerable degree of development when it enters the uterus from the Fallopian tube. All the earlier steps in development are directed towards the formation of the structure necessary for the protection of the embryo—the chorion, amnion, yolk sac, allantois and placenta.

CHAPTER III.

THE PRIMITIVE STREAK, NOTOCHORD AND SOMITES.

Law of Recapitulation.—The pioneers of Embryology began in the hope of discovering the stages in the evolution of the human body by an accurate study of its development. It was expected that the ovum, as it became transformed into the embryo, and the embryo as it changed into the foetus, would recapitulate man's evolutionary history. From what has been related in the two previous chapters it is plain that we see no resemblance between the successive stages of the human embryo and the succession of types which compose the scale of the Animal Kingdom. Those who expected the law of recapitulation to hold true in all its details forgot that the human embryo is radically modified in order that the first nine months of development may be spent parasitically in the womb of the mother. The storage of yolk in the ovum, the precocious development of trophoblast, chorion, amnion and allantois, have transformed the orderly manifestation of evolutionary stages. Yet to a certain degree the law remains true; the human body begins as a single cell, similar in constitution to the simplest form of animal life—a protozoon; it becomes a globular cluster of cells in its morula stage, similar to the simple forms of multicellular organisms. Further, there are numerous features seen during the development of the embryo which can only be explained by supposing that the human body, in the course of its evolution, has passed through those stages which we see represented in simpler Invertebrate forms—such as the Hydra and the worm. The first of these obscure embryonic manifestations is the primitive streak and groove.

The Primitive Streak.—In the third week when the embryonic plate lies on the upper surface of the yolk sac and measures only about 1 mm. ($\frac{1}{5}$ in.) in length, there appears along the median line of its hinder half a linear demarcation known as the primitive streak. This line becomes the site of developmental processes of the highest significance. No sooner has the primitive streak appeared than there is formed a perforation or canal at its cranial or anterior end—the **neurenteric canal** (Fig. 35, *A*). If a section is made across the embryonic plate at the site of the canal, the entoderm lining the archenteron is seen to be continuous with the ectoderm on the dorsal surface of the plate, the cavity of the primitive gut thus opening or having a mouth, on the dorsal surface of the embryo (Fig. 34, *B*). If a section be made further back, across the region of the primitive streak (Fig. 34, *C*) it is seen that the entoderm fuses with the ectoderm and that,

at the line of fusion the mesodermic plates are continuous with both entoderm and ectoderm. Along the line of fusion there is a vigorous production of mesoderm. A section in front of the neurenteric canal (Fig. 34, A) shows still other appearances; the ectoderm, now being differ-

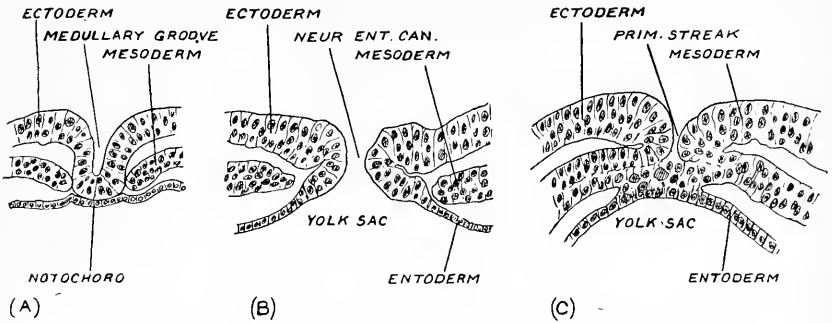


FIG. 34.—Section across a human embryonic plate measuring 1.5 mm. in length. (Graf Spee.)

- A. In front of the neurenteric canal.
- B. At the neurenteric canal.
- C. Across the primitive streak, behind the neurenteric canal.

entiated into the neural plate, is moulded to form the rudiment of the medullary furrow; beneath the furrow there is a plate of cells—the **notochordal plate** (Fig. 34, A) which although apparently continuous with the entoderm is yet of different origin. The notochordal plate will form the

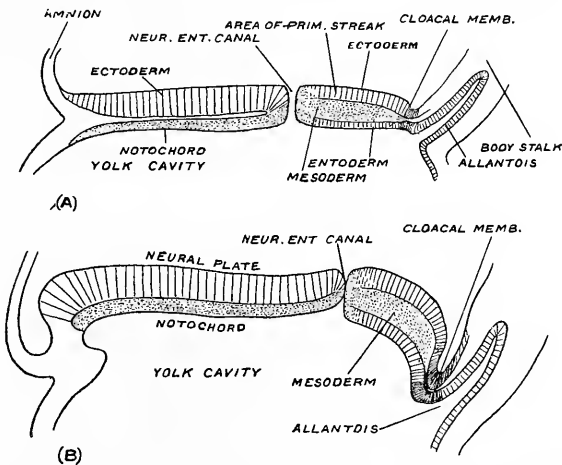


FIG. 35.—Sections along the median line of two embryonic plates, figured by Graf Spee, to show the shifting backwards of the neurenteric canal and primitive streak as growth takes place.

notochord, the supporting or skeletal rod of the medullary plate. At the neurenteric canal and in front of it the mesoderm is no longer continuous with the ectoderm or entoderm; it has grown forwards from the site of production at the primitive streak.

If sections are made along the embryonic plate (Fig. 35, *A* and *B*) further light is thrown on the relationship of the neurenteric canal and primitive streak to the growth of the embryo. In Fig. 35, *A* the neurenteric canal is seen to be placed near the middle point of the plate—which has a total length of a little over 1 mm. while in the older embryo which measures 1.7 mm. in length, it is pushed backwards by the rapid growth and extension of the precanalicular part of the embryonic plate. The region of the primitive streak—the postcanalicular part of the embryonic plate—although the site of mesodermal production, has undergone a lesser degree of growth and is being pushed to the hinder end of the embryonic plate. The exact manner in which the precanalicular part expands we are not certain of, but it will be noted that at the anterior lip of the neurenteric

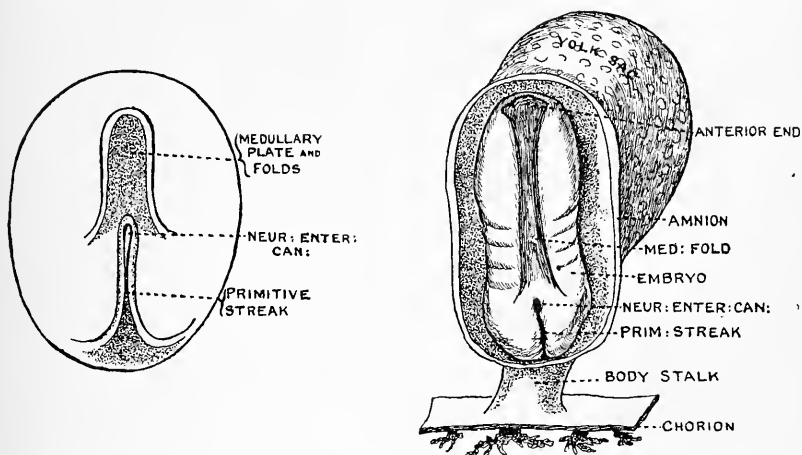


FIG. 36.—Diagram of the Embryogenic area of an Embryonic plate viewed from above.
 FIG. 37.—The Medullary Plate and Primitive Streak on an Embryo towards the end of the 3rd week. (After Graf Spee.)

canal the neural plate becomes continuous with the notochordal plate and we suspect that this lip represents a growing edge. The first formed part of the precanalicular plate represents the hinder cranial region; as the plate grows the neurenteric canal moves backwards through the cervical and dorsal regions until it reaches the lumbar region early in the fourth week, the embryo then being less than 3 mm. in length. If, as sometimes occurs, the neurenteric canal remains unclosed, a fistula from the bowel opens on the lumbar region of the back. In Fig. 34 it will be seen that while the neurenteric canal lies at the anterior end of the primitive streak a very important structure—the **cloacal membrane**—marks its posterior end. The cloacal membrane, lying at the foot of the body stalk, marks the site of the anus and vulval cleft. Thus the whole of the hinder end of the human body is developed on each side of the primitive streak, a relationship which must be understood if certain malformations of the human body are to be adequately explained.

In the third week of development, when the primitive streak is being pushed backward on the embryonic plate, the medullary folds appear

on its anterior part, the hinder ends of the folds, as they spread backwards, coming to enclose the neurenteric canal and anterior end of the primitive streak (Fig. 37). The early relationship of the medullary folds to the primitive streak is shown diagrammatically in Fig. 36. It will be seen that as the medullary folds invade the postcanalicular part of the plate the neurenteric canal and anterior end of the streak will be included within them and eventually lie in the hinder part of the spinal cord. The hinder end of the streak is carried away from the cloacal membrane by the formation of the tail.

The Blastopore.—The primitive streak with the neurenteric canal at its front end and the cloacal membrane at its hind, can be best explained by supposing that they represent the primitive mouth or blastopore of lower invertebrate animal types. Its formation in the vertebrate body is

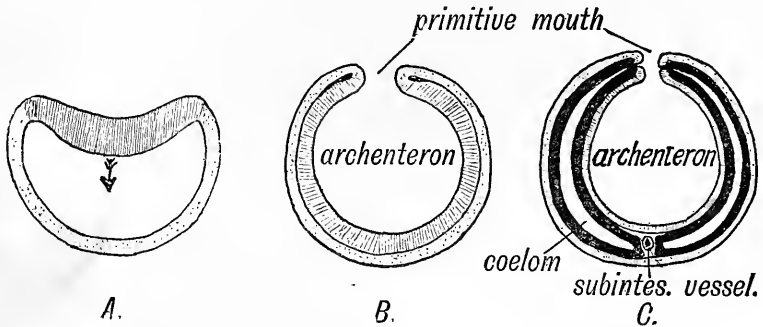


FIG. 38.—Diagram showing three stages in the early development of *Amphioxus*.

- A. Invagination of the entoderm (shaded) within the ectoderm (stippled).
- B. Formation of archenteron and primitive mouth (blastopore).
- C. Origin of mesoderm (black) and coelom from margin of primitive mouth, with formation of a ventral mesentery round the subintestinal vein. (After Robinson.)

best studied in amphioxus (Fig. 38). At an early stage of its segmentation the ovum of this animal forms a hollow sphere (Fig. 38, A); one part of the sphere becomes invaginated to form the entoderm, the uninvaginated or outer layer becoming the ectoderm. The brim of the bilaminar flask (gastrula or cup) thus formed served as a mouth or blastopore to the cavity of the entoderm (archenteron) (Fig. 38, B). The primitive streak and groove seen in the embryos of all vertebrates are believed to arise from a linear fusion of the lips of the blastopore. The neurenteric canal is a part of the blastopore which retains its patency for a few days only in the human embryo. The process of invagination or gastrulation, which is seen to occur in the development of amphioxus—by far the most primitive of vertebrate forms—has become masked and obscured in the embryos of higher vertebrates. The process has been profoundly modified by the accumulation of yolk in the ovum and the precocious development of the embryonic membranes. The embryonic plate situated on the archenteron (Fig. 37) may be regarded as the modified gastrula stage of amphioxus and the primitive streak as a modified blastopore. We shall see that

some of the primary processes of development are initiated at the margins of the primitive streak.¹

Origin of the Mesoderm and Coelom.—In the developing ova of higher vertebrates the mesoderm is known to originate at each side of the primitive streak, but it is difficult to follow the exact manner of its development (Fig 34, C). In amphioxus it arises as a bilateral series of diverticula from the margin of the gastrular mouth or blastopore, along the line at which the ectoderm and entoderm are continuous (Fig. 38, C). The diverticula expand and their cavities fuse together between the two primary layers to form the coelom ; the right and left series of diverticula meet below the archenteron and form a ventral median mesentery (Fig. 38, C). In higher vertebrate ova, the ectoderm and entoderm are fused together along the primitive groove just as round the primitive mouth of a Hydra. The mesoderm arises, as we have seen, from the line of union, and spreads outwards between the two primary layers. The coelom is formed, not as a diverticular cavity, but by a cleavage of the mesoderm, into outer and inner layers. In the human embryo the mesoderm appears at an extremely early stage ; long before the primitive streak has been formed mesoderm appears in the human blastocyst (see Fig. 15, p. 13). The coelom appears first as a cleavage of the blastocystic mesoderm (Fig. 16, p. 14), so altered have developmental processes become owing to the early formation of the ectodermal wall in the human ovum yet the primitive streak remains the chief site of mesodermal production.

Differentiation of Mesoderm.—In Fig. 39, a diagrammatic representation is given of the parts into which the mesoderm, and the cavity of the

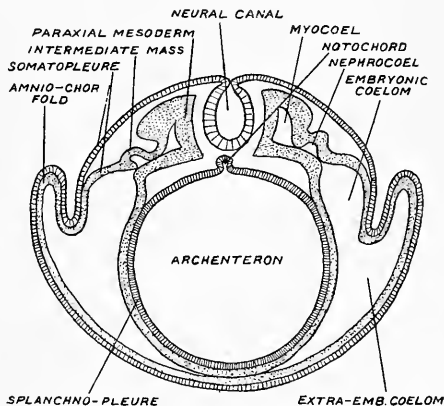


FIG. 39.—Diagrammatic section across a vertebrate embryo to show the parts of the mesoderm, of the coelom, and also the origin of the neural canal and notochord.

mesoderm—the coelom—become differentiated. Along each side of the medullary tube lies the paraxial mesoderm ; that part we shall see becomes

¹ For details relating to the nature of the blastopore see *Text-Book of Embryology*. Vol. I. *Invertebrata*, by Prof. E. W. MacBride. Vol. II. *Vertebrata*, by J. Graham Kerr, 1919 ; Profs. J. T. Wilson and J. P. Hill, *Phil. Trans.* 1908, Ser. B, vol. 199, p. 31 ; The late Dr. R. Assheton, *Quart. Journ. Mic. Sc.* 1910, vol. 54, pp. 221, 631,

divided into somites and gives rise to muscles and vertebrae; lateral to the paraxial mass, comes the intermediate cell mass; then, lateral to the intermediate mass in which the urino-genital glands are formed, the mesoderm is cleft into an outer and inner layer—one joining the ectoderm to form the somatopleure, the other, the entoderm, to form the splanchnopleure. The cleft between these laminae is the coelomic space; part becomes enclosed within the embryo to form the pericardial, pleural and peritoneal cavities; the extraembryonic part (Fig. 39) is carried away and obliterated between the foetal membranes. Within the intermediate cell mass and within the paraxial mass there are extensions of the original coelom—known as the nephrocoel and myocoel. From the mesoderm arise the great mass of tissues which constitute the human body—the tissues of locomotion—muscles, bones, ligaments

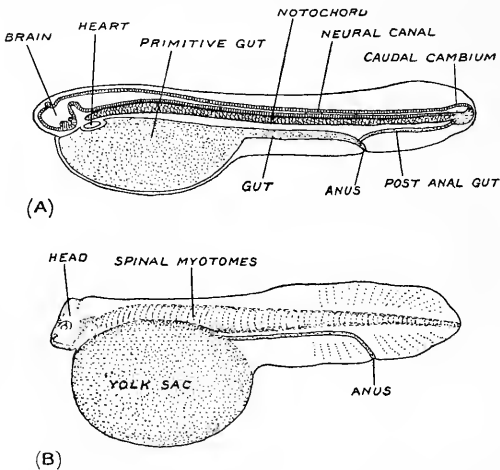


FIG. 40.—*A.* Diagrammatic longitudinal section of a larval *Polypterus*—a ganoid fish—to show the relations of the notochord. (After Graham Kerr.)
B. The larval form of *Lepidosteus*, another ganoid fish, to show the segmented vertebral musculature covering the notochord. (After Graham Kerr.)

and connective cells. And also the circulatory and mobile systems—the heart, blood vessels, blood cells of all kinds and all forms of moving tissue cells. To this latter element of the mesoderm—the cells which form vessels, blood, connective tissue and mobile cells is given the name of **Mesenchyme**.

Notochord.—In its origin the notochord, the forerunner of the spinal column, is closely related to the primitive streak (see Fig. 40, *A*). Amongst the structures produced at its anterior end where the ectoderm turns in to join the entoderm is a plate of cells which comes to lie along the median line on the roof of the archenteron or primitive gut-cavity (Fig. 35). Presently the plate becomes folded off from the roof of the archenteron (Fig. 39) to form a rod of peculiar cells—the notochord. The posterior part of the notochord never forms part of the gut-cavity, but is developed from the lateral margins of the primitive streak. It will thus be seen that

the first representation of a skeleton is produced at an extremely early date, and that it appears as a support for the medullary plate when that plate is folded in to form a tube. Its continuity with the primitive gut seems accidental, for it is hard to believe that a mesodermal skeletal structure such as the notochord could have been evolved from the alimentary system.

Segmentation.—We have seen that the medullary folds rise up towards the end of the third week of development when the embryonic plate is only about 1.5 mm. in length. No sooner do they commence to fuse and thus enclose the neural plate than that part of the mesoderm which has been laid down by the side of the neural tube—the paraxial mesoderm (Fig. 39) begins to be divided, from before backwards, into segmental blocks or **somites**. Segmentation which begins at what will become the occipital region of the head, is confined to the paraxial mesoderm. In the embryo shown in Fig. 19, p. 17, five somites have been formed; by the end of the fourth week, when the embryo has grown to a length of about 3 mm. (Fig. 20) the process has reached the first caudal or coccygeal segment, there being at this time 3 occipital and 30 body somites. Thereafter segmentation proceeds slowly in the caudal region, there being 8 or 10 caudal somites at the end of the sixth week, when the tail has reached its maximum development and the embryo is about 11 mm. long.

To understand the meaning of segmentation we must again appeal to comparative anatomy. Segmentation marks the onset of vertebral characterization in the human embryo. In Fig. 40, *A* a diagrammatic longitudinal section of a fish larva is reproduced to show the relations of the notochord; it and the neural tube we have seen are formed first in the head region and then grow backwards. In Fig. 40, *B* another fish larva is depicted, with the notochord clothed with muscle segments or myotomes. A mere glance at such diagrams shows that the notochord or primitive vertebral column and the segmented spinal musculature represent a great sculling apparatus—the locomotory machine of the lowest and oldest vertebrates. Gill arches also appear in the human embryo very soon after segmentation has commenced (see Fig. 20), but even without their guidance one would infer, on the evidence of segmentation alone, that the human embryo in the fourth week is passing through a fish stage and that our vertebral column and spinal musculature represent a former locomotory system. The **gill-segmentation** is different and apparently older than the body-segmentation; and as we shall see, the gills are not fashioned out of the paraxial mesoderm.

Experimental Embryology.—In recent years those who study the development of the body have resorted to experiment in order to obtain a more direct knowledge of the laws and conditions of development. Loeb has shown that the ova of some invertebrate animals may be stimulated to development by chemical substances which thus simulate the action of spermatozoa. Dareste, fifty years ago, discovered that eggs hatched at abnormal temperatures often gave rise to malformed embryos. In more recent years it has been discovered that the addition of certain salts

produces one form of malformation, while another group of salt solutions added to the water, in which the embryos of invertebrate animals are being hatched, will produce another set of abnormalities. Stockard¹ discovered that the addition of magnesium chloride to the sea water in which fish-embryos are being hatched will lead to half of the larvae becoming cyclops. It has been found that embryonic structures can be transplanted or grown on artificial media. The original experiments of Dr. Ross Harrison,² in which he transplanted and studied parts of the living embryonic spinal cord, did much to open up this method of enquiry. In embryonic structures thus transplanted the development of nerve and other cells has been successfully studied. It has also been found that by dividing the ovum at an early stage after fertilization, or by separating the cells, it is possible to produce, in lower animal forms, an embryo from each part or cell separated, but the embryos so produced are small in size, and do not reach adult life. In other cases the cells thus separated only produce part of an embryo. Those who wish to obtain information on this important branch of embryology will find some of the more recent papers by Ross Harrison, W. H. Lewis and others in the *American Journal of Anatomy* and *Anatomical Record*.

Twins, Perfect and Imperfect.³—The study of early stages in the development of the ovum throws some light on the manner in which twins arise, and especially on the production of human monsters by the incomplete separation of twins. Three theories are held concerning the production of Twins: (1) There may be two or more ova shed and fertilized. (2) That each of the cells produced by the first division of the ovum gives rise to an embryo. Assheton found two inner cell masses in the blastocyst stage (Stage II.) of a sheep, each of which would have formed an embryo. A blastocyst is necessarily the product of one ovum. (3) Beard regards the cells formed by the early divisions of the ovum as indeterminate in nature—a **thallus** from which a brood of germinal cells are produced. One of these germinal cells becomes the embryo, in the genital ridges of which the remaining germ cells find a nidus and form ova or spermatozoa. If two of these germinal cells become embryos, twins are produced, if three, triplets. Twins are produced once in every 89 births, but it is probable that twin pregnancies are more frequent than is suggested by birth statistics. Dr. Streeter found a vestigial twin in a human pregnancy of the third week.⁴ Dr. Crawford Watt⁵ has described a normal twin pregnancy of the fourth week.

¹ *Journ. Exper. Zool.* 1909, vol. 6, p. 285.

² *Ibid.* 1907, vol. 4, p. 239.

³ For literature on malformations of the body see: J. W. Ballantyne, *Antenatal Pathology*, London, 1904; *Die Morphologie der Missbildungen des Menschen und der Tiere*, edited by Ernst Schwalbe, Jena, 1906-1912; Prof. F. P. Mall, *Journ. of Morphology*, 1908, vol. 19, p. 3 (Description of a large collection of malformed human embryos with references to the more recent literature on the causation of the various kinds of maldevelopment). Also, later, *Amer. Journ. Anat.* 1917, vol. 22, p. 49.

⁴ *Contributions to Embryology*, 1920, vol. 9, p. 389.

⁵ *Ibid.* 1915, vol. 2, p. 5.

“Identical” twins¹ are produced by the division of a single ovum. They are contained within the same enveloping membranes, are of the same sex and so alike in features that, to the casual observer, they are hard to distinguish. In the production of identical twins, the embryonic plates (see Figs. *A*, *B*, *C*) may remain unseparated, and in this manner most of the numerous forms of human monsters are produced. The embryos may remain attached to a common yolk sac, thus forming a “Siamese” twin—the two individuals remaining attached in the region of the umbilicus. The union may affect only the lower body and limbs, or only the upper part and arms. All kinds and degrees of union occur—head to head, buttocks to buttocks, but the most common is a ventral union effected through a common yolk sac. In some cases one twin becomes a “parasite,” and dependent on the other—the “host” twin—for its circulation and nourishment. Only part of the parasitic twin

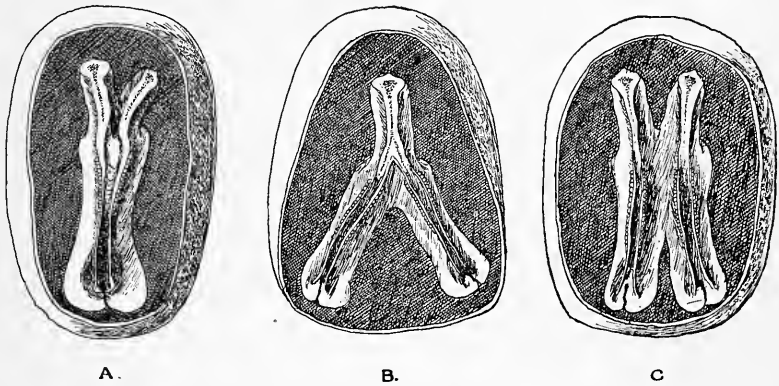


FIG. 41.—Division of the Embryonic Plate, forming imperfect twins.
A, Anterior dichotomy; *B*, posterior dichotomy; *C*, intermediate union.

may develop, and then remains attached as an appendage to the body of the host twin. At an early stage of development the parasitic twin, arrested and delayed in development, may become included within the body of the host twin. There are two examples of this condition in the Museum of the Royal College of Surgeons, England.

Duplication and Atrophy of Parts.—Parts of the body, such as a digit or the penis may be duplicated. In such cases we suppose that the group of cells which give rise to the part undergo a division or dichotomy, just as the growing point of a plant stem may undergo branching. Those parts of the body which arise as outgrowths, such as the nasal processes, the extremities, or segments of the extremities, may be partially or completely arrested at a very early stage of development. The embryo itself may be retarded in development or completely blasted while the membranes go on developing, giving rise to the developmental product known as a

¹ D. Berry Hart, *Proc. Roy. Soc. Edin.* July 1909; J. F. Gemmill, *Teratology of Fishes*, Glasgow, 1912; G. W. Tannreuther, *Anat. Rec.* 1919, vol. 6, p. 355.

“mole.” It is known that if eggs are incubated in abnormal conditions as regards temperature or atmosphere, such malformations occur more frequently than usual. Practically nothing is known of the circumstances or influences which give rise to abnormalities in the Human Embryo. We know that such abnormalities tend to occur in certain families; they are hereditary, but we do not know the circumstances which give rise to them.

Knowledge relating to deformed and monstrous foetuses is known as **Teratology**. Mention will be made of various congenital deformities as we proceed.

CHAPTER IV.

THE AGE CHANGES IN THE EMBRYO AND FOETUS.

IN Chapter I., having followed the developmental changes in the human embryo during the first five weeks, when it had reached a crown-rump length of 5 mm. ($\frac{1}{5}$ in.) and the condition of parts shown in Fig. 42, we had to break away in Chapters II. and III. to note the manner in which it

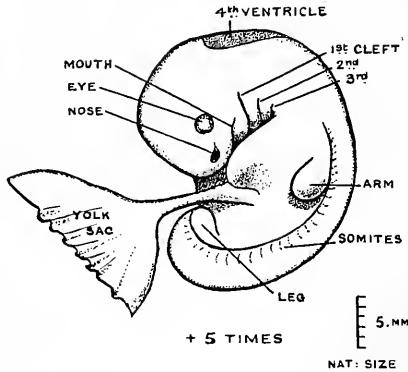


FIG. 42.—Outline of a Human Embryo 5 mm. in length, and in the 5th week of development. (Reconstructed by Professor Keibel and Dr. Elze.)

effected a lodgment in the uterus and to examine certain processes which give rise to fundamental parts of the embryonic body. In this chapter we return to trace the further history of the embryo, to watch it becoming transformed into a foetus and to register the subsequent changes during the nine months it spends in its mother's womb.

In recent years our knowledge concerning the rate at which the human embryo grows and the stages through which it passes week by week has become more accurate. This is largely due to the work accomplished by the late Prof. Mall¹ who collected facts relating to all cases where the age of an embryo had been ascertained and by tabulating his data was able to estimate the size and stage of development reached by an average human embryo week after week. His main results, so far as concern the first two months, are set out in Fig. 43, taken from an article written by his

¹ See his last paper on this subject, *Amer. Journ. of Anat.* 1918, vol. 23, p. 397.

distinguished pupil—Prof. Herbert Evans. Six stages of development are represented: at the end 3rd, 4th, 5th, 6th, 7th and 8th weeks. Under each embryo is given the mean length it should reach at a certain date, but it has to be remembered that the rate of growth will vary in embryos and foetuses just as in children, and that some will be precocious while others will be backward. The measurements relate to fresh specimens, for when embryos are preserved and prepared for microscopic examination they shrink in size. It is convenient to regard 3 mm. as measured from the crown to the rump of the embryo as marking the end of the fourth week, and 5 mm. as an index of the end of the fifth week of development. In the 6th, 7th, and 8th weeks the embryo adds almost one millimetre to its

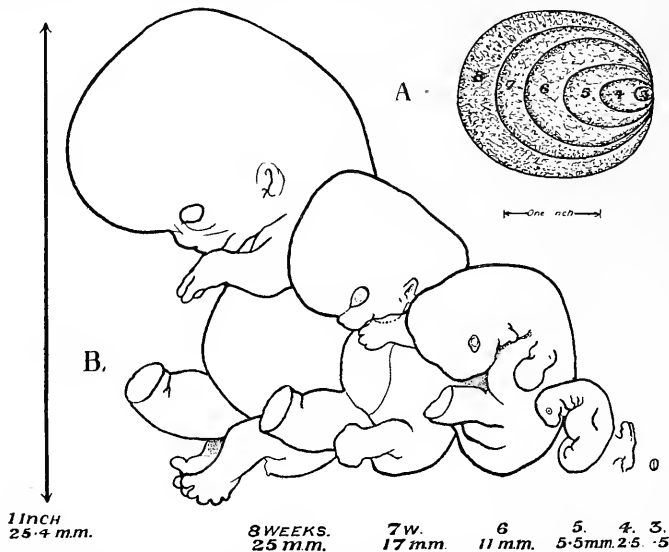


FIG. 43.—Series of six drawings illustrating the stages of growth from the end of the 3rd week to the end of the 8th. In a corner of the figure is a diagram to illustrate the rate of growth of the chorionic vesicle at corresponding dates. (Prof. H. M. Evans.)

length daily, being about 25 mm. (1 inch) at the end of the 8th week. Hence we may readily estimate the age of an embryo or foetus under 25 mm. in length, by regarding the first 5 mm. as representing 35 days' growth, and adding a day for every additional millimetre of its length. For example, the age in days of an embryo measuring 15 mm. in length would be estimated thus: 5 mm. = 35 days + 10 for the additional 10 mm. = 45 days. In the 9th, 10th, 11th, 12th, 13th and 14th weeks—up to the end of the 3rd month—when the crown-rump length amounts to 100 mm. (4 in.)—the daily rate of growth is approximately 1.5 mm.

External Changes in the 6th week.¹—As may be seen by comparing Figs. 42 and 44, the 6th week constitutes a period of rapid transformation.

¹ See specimens described by J. L. Bremer, *Amer. Journ. Anat.* 1905, vol. 5, p. 459; C. Elze, *Anat. Hefte*, 1907, vol. 35, p. 409; N. W. Ingalls, *Archiv. f. mikros. Anat. und*

Not only does the length of the embryo increase from 5 mm. to 11 mm. but there are very definite changes in the form of its external parts. At the end of the 5th week the gill-arch system of the primitive pharynx is at its height, four arches being distinguishable; in the 6th week the 3rd and 4th arches sink into a pit in the neck—the **cervical sinus**—(Fig. 44), while the 2nd or hyoid arch grows backwards over the pit and thus hides the hinder arches. Here we are witnessing the closing in or operculation of the branchial arches—as it takes place in gill-bearing vertebrates. Even at the close of the 6th week the face is represented merely by a

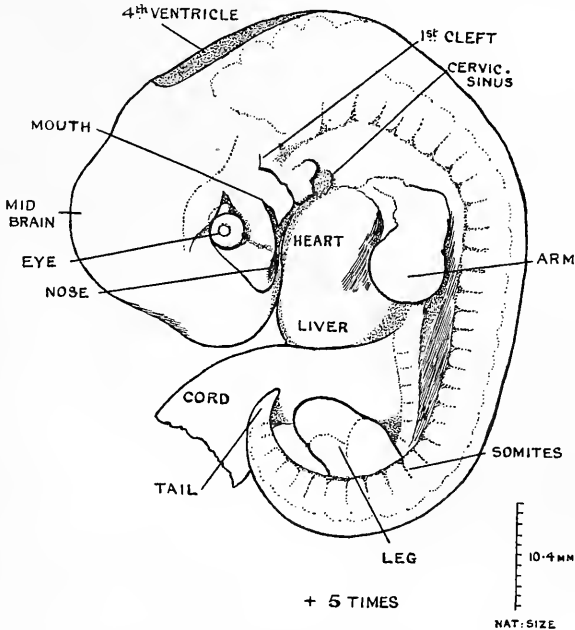


FIG. 44.—Outline of a Human Embryo 10.4 mm. long and in the 6th week of development. (After Broman.) (Magnific. $\times 5$.)

forehead filled out by the relatively small forebrain vesicle; behind and under the forehead are seen the nasal, maxillary and mandibular processes which will give rise to the face proper. All of these elements have made headway during the 6th week (Figs. 42, 43, 44). The head region even in the 6th week is still tubular in form; the mid and hind brains form the greater part of the central nervous system, for the cerebral vesicles have as yet only begun to grow out from the fore brain. The limb buds, which in the 5th week were still undemarcated into segments, now show their three primitive parts—upper arm and thigh, forearm and leg, and a plate-like hand and foot. In point of differentiation the forelimb is always in

Entwick. 1907, vol. 70, p. 506; L. Frassi, *Ibid.* p. 492. Dr. H. L. Barniville gives a full description of an 8.5 mm. Embryo, *Journ. Anat.* 1915, vol. 49, p. 1. Dr. F. W. Thyng gives excellent figures of one measuring 17.8 mm., *Amer. Journ. of Anat.* 1915, vol. 17, p. 51.

advance of the hind. At the close of the 6th week the first appearance of webbed digits can be detected, and at the same time, when the length of the embryo is about 11 mm. the tail reaches its maximum development (Fig. 44); in the 7th week retrogression has already set in. The umbilical cord becomes lengthened and more clearly differentiated in the 6th week; between the attachment of the cord to the ventral wall of the embryo and the gill-formation of the primitive pharynx is seen the bulging eminence of the heart (Fig. 42); below the heart eminence, as may be seen in Fig. 44, there appears in the 6th week a second eminence, that caused by the developing liver.

Embryo-Foetus.—During the 7th week the embryo becomes a foetus—the transformation being well shown in Fig. 43. In its crown-rump length the embryo expands from 11 to 17 mm., but the characteristic changes

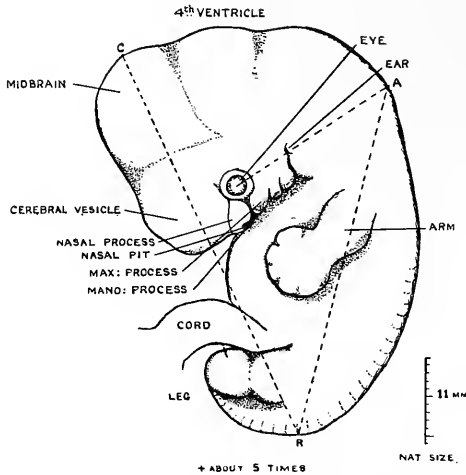


FIG. 45.—Outline of an embryo, although only 11 mm. long, yet showing changes characteristic of an early stage of the 7th week. (After Broman.)

The line *C-R* indicates the manner in which the crown-rump diameter is measured; the line *A-R* shows the neck-rump length, *A* being found by drawing a line backward through the rudiments of the eye and ear.

are seen in the face, head and limbs. An early stage of the 7th week is shown in Fig. 45; the basal parts of the face are being laid down. Under the eye are seen the nasal processes carrying the open nasal cavities backwards into the region of the mouth, while growing forwards beneath the eye are to be observed the maxillary processes which will provide the bases of the upper jaw. Still further back in the pharynx (Fig. 45) are seen two comparatively small processes—the mandibular (1st arch) and hyoid (2nd arch). Behind the hyoid arch there is a depression marking the cervical sinus. By the end of the 7th week (Fig. 43) the nasal, maxillary and mandibular processes have united to form a relatively small face; at the upper end of the postmandibular cleft has appeared the rudiment of an ear. The changes in the head itself are also apparent; at the end of the 7th week the cylindrical cranial form is being replaced by one more

distinctly globular; the forehead in particular has become enlarged. These changes are due to the rapid expansion of the cerebral vesicles during the 7th week. The changes in the limbs are also very evident; they are now folded on the belly-wall, palm towards palm and sole towards sole; the digits are demarcated. The tail is disappearing. The head is no longer bent forwards with the forehead touching the root of the umbilical cord, but is lifted up, for the embryonic flexure of the cervical region is being undone and a narrowing of the post-cranial region to form a neck becomes apparent. The heart is now completely divided into right and left chambers and the growth of the neck is lifting the pharyngeal region away from the heart. With these changes in the facial region, in the head, neck, limbs and heart the embryo of the 6th week becomes the foetus of the 7th. One other very important event also characterises this stage of transformation: the **cellular blastema of the skeleton** begins to change into cartilage and into bone. It also becomes possible to distinguish the ovary from the testicle.

Changes in the 8th week.—At the end of the 8th week the crown-rump diameter measures about 25 mm. (1 inch). The changes of this week are a continuation of those we have just described (Fig. 46); the

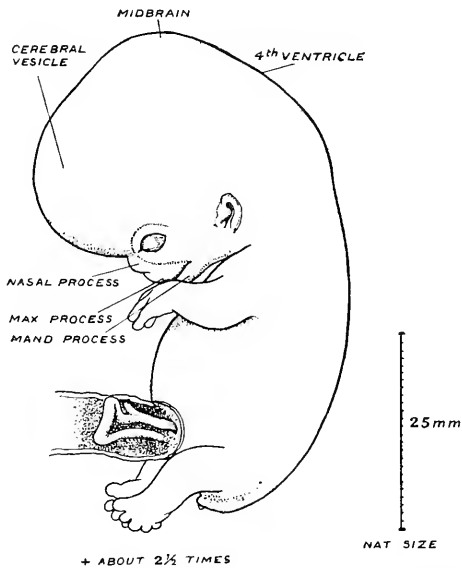


FIG. 46.—Outline of a Foetus 22 mm. long, and at the end of the 2nd month of development. (After Broman.)

nasal and maxillary processes have fused to form the upper face; the upper lip is completed, but the palatal processes have not yet separated the buccal from the nasal cavities. The cerebral vesicles are expanding rapidly backwards; the neck is being differentiated and the limbs are making progress. The rudiment of the external genital organs is ap-

parent, but as yet gives no clue to sex. The intestinal loop lies within the root of the umbilical cord. Henceforward, until the end of gestation, the chief changes are those of growth.¹

The Full-Time Foetus.—We speak of the period of human gestation—the time spent by the human young in the uterus of the mother, preparatory to an independent existence—as being one of 9 months, and if by a month we mean 30 days—270 days in all—we are as near the truth as our present evidence will take us. Medical men can seldom discover the exact date of conception and hence to get a fixed point for a reckoning they begin their estimate counting from the first day of the mother's last menstrual period, and taking this day as a fixed point, count that parturition will take place 280 days hence. Observations made on cases where the date of impregnation may be inferred show that the actual *mean* period of gestation is 270 days. The 270th day is the bull's-eye at which Nature aims, but even the best of marksmen make "inners" and "outers," and it is so in all of Nature's shootings. She is ever subject to the law of chance; hence in all developmental and growth manifestation we meet with variation round a mean.

By the 270th day the foetus has attained a weight of about 7 lbs. and a height, if we measure from crown to rump (sitting height), of 336 mm., but if we include the lower extremities (standing height) the measurement is 500 mm. (nearly 20 inches). It sometimes happens that birth takes place at the end of the 7th month when the foetus weighs between 4-5 lbs. and in its standing height measures 400 mm. or less, its sitting height being then about 265 mm. In such premature children, who have always a defective heat-regulating mechanism, it will be observed that the tips of the nails just reach the ends of the nail beds, whereas in the full-time child the nail edges are free and projecting. The full-time child has also an outcrop of hair on the head; lanugo—foetal hair—can be detected on various parts of the body. The hair tips which break on the surface of the skin about the end of the 4th month may be plentiful on the scalp at the end of the 7th, but the skin is then of bright lobster-red, the subcutaneous tissue is less stored with fat and the sebaceous covering, known as the *vernix caseosa*, forms a thin and unequal coating.

¹ For changes in 9th week see F. E. Blaisdell, *Journ. Anat.* 1914, vol. 48, p. 182.

Table of Growth.—It is impossible for anyone to remember the dimensions reached during the various stages of foetal development and growth, but it is often convenient to have a table of measurements for reference. The one given here was prepared by the late Prof. Mall¹:

CROWN-RUMP LENGTH.	STANDING HEIGHT.	AGE IN WEEKS.	AGE IN DAYS.
.5 mm.	—	3	21
2.5 "	—	4	28
5.5 "	—	5	35
11 "	—	6	42
17 "	—	7	49
25 "	—	8	56
32 "	—	9	63
43 "	—	10	70
53 "	—	11	77
68 "	—	12	84
81 "	—	13	91
100 "	149	14	98 end of 3rd month.
111 "	—	15	105
121 "	—	16	112
134 "	—	17	119
145 "	223	18	126 end of 4th month.
157 "	—	19	133
167 "	—	20	140
180 "	—	21	147
192 "	295	22	154 end of 5th month.
202 "	—	23	161
210 "	—	24	168
220 "	—	25	175
230 "	331	26	182 end of 6th month.
237 "	—	27	189
245 "	—	28	196
252 "	—	29	203
265 "	400	30	210 end of 7th month.
276 "	—	31	217
284 "	—	32	224
293 "	—	33	231
301 "	443	34	238 end of 8th month.
310 "	—	35	245
316 "	—	36	252
325 "	—	37	259
336 "	500	—	270 end of 9th month.

¹ See reference, p. 45.

CHAPTER V.

THE SPINAL COLUMN AND BACK.

Stages in the Development of the Spinal Column.—In previous chapters the main facts relating to the development of the human body during the first and second months have been briefly sketched. We now turn to the consideration of particular parts of the human body, and naturally take up first the vertebral column—the main axis of the body. The most primitive form of axial support—the notochord—appears in the embryo during the third week. In amphioxus the notochord forms a permanent structure; in all vertebrate animals it is replaced by a segmented or vertebral axis. In the evolution of the spinal column three stages are recognized: (1) one in which the skeletal segments were composed of cellular or mesenchymatous tissue; (2) a cartilaginous stage, in which the cells of the mesenchyme (see p. 40) become modified into cartilage-forming or chondrogenous cells; (3) a final stage where the cartilage is replaced by bone. In the human embryo we see those three stages appear in succession; at the beginning of the second month the membranous foundation of the vertebra is being laid down; in the middle of that month the cartilaginous change has commenced; by the beginning of the third month ossification has commenced. In only certain groups of fishes is the cartilaginous stage a permanent one.

Stages in the Evolution of the Human Spinal Column.—We have already seen that the vertebral column and its muscles appear first as a great flexible scull for driving the animal forwards (p. 41), but in nearly all mammals the vertebral column comes to serve as a horizontal axis or arch, which is supported on the fore and hind limbs. In a small group, however, which includes the anthropoid apes and man, the spinal column no longer forms a horizontal but a vertical axis or column. These higher primates are upright or **orthograde** when they move, in contradistinction to the ordinary four-footed mammals which are **pronograde**. There is no doubt that the orthograde posture was evolved from the pronograde. Although the anthropoid apes are orthograde, yet they use their arms in locomotion, to assist their lower extremities in supporting the weight of their bodies. Man is also orthograde, but he differs from the anthropoids in supporting the weight of his body entirely on his lower extremities. Hence we find that the spinal column of man, although similar to that of the anthropoids, shows many peculiar adaptations to his manner of locomotion. These adaptations become especially manifest as

the child learns to walk, and are best realized by a survey of the pyramids and curves of the spine.

The Pyramids of the Spine.—The spine, when viewed from the front, is seen to be made up of four pyramids: (1) Cervical; (2) upper dorsal; (3) dorso-lumbar; (4) sacro-coccygeal (Fig. 47). The bases of the two upper pyramids meet at the disc between the 7th cervical and 1st dorsal vertebrae; the bases of the lower two at the disc between the 5th lumbar and 1st sacral vertebrae. The apices of the two middle pyramids meet at the disc between the 4th and 5th dorsal vertebrae, which have therefore the narrowest bodies of the vertebral series. The narrowing in the upper dorsal region is due to the fact that the weight of the upper half of the trunk is partly borne by, and transmitted to, the lower dorsal region by the sternum and ribs which thus relieve the spine to some extent (Fig. 47). At the sacrum the weight is transferred to the pelvis and lower limbs, hence the rapid diminution of the sacrum and coccyx. A well-marked thickening or bar in each ilium runs from the auricular surface to the acetabulum and transmits the weight to the femora.

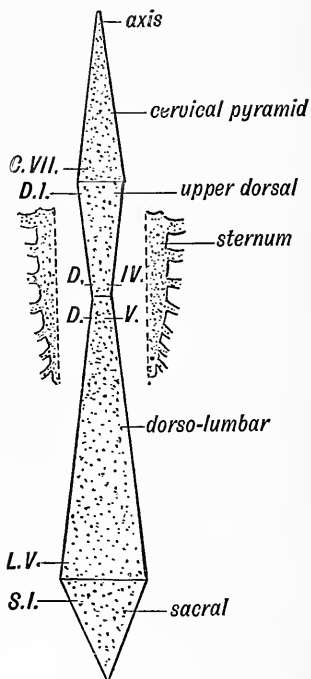


FIG. 47.—Diagram of the Pyramids of the Spine.

The Curves of the Spinal Column.—

There is only one curve—an anterior concavity—until the 3rd month (Fig. 48, *A*). About the beginning of the 4th month the sacro-vertebral angle forms between the lumbar and sacral regions (Fig. 48, *B*). At birth the cervical and sacral curves have appeared, but the sacral not to a pronounced extent (Fig. 48, *C*). The lumbar curve appears as the child learns to walk. It is produced to allow the body to be brought vertically over the lower extremities. The sacral and cervical curves also become at that time more marked (Fig. 48, *D*). The dorsal curvature and the sacro-vertebral angle are the primitive curves and are present in all mammals. The others are adaptations to the upright posture. The lumbar curve is most pronounced in the highly civilized races.

Proportion of Cartilage and Bone.—The intervertebral discs form one-third of the total height of the spine; the proportion of cartilage is greater in the lumbar than in the dorsal region and greater in the dorsal than in the cervical. The lumbar and cervical curvatures are due chiefly to the shape of the discs (H. Morris). In the lumbar region, which is convex forwards, only the lower three vertebrae are deeper in front than

behind. This is true only for the higher races of mankind, for as Cunningham has shown, in lower races, as in the gorilla, only the last lumbar vertebra is deeper in front than behind, and thus helps to maintain the lumbar curvature.

Unstable Regions of the Spine.¹—In about 90 % of men there are 7 cervical, 12 dorsal, 5 lumbar, 5 sacral and 4 caudal vertebrae, making 33 in all. In the remaining 10 % there is some departure from the normal arrangement and these departures affect certain definite regions. The regions affected are those which lie at the junction of one section of the spine with another—at the cervico-dorsal, dorso-lumbar and lumbo-sacral junctions. At an early stage of development all the vertebrae

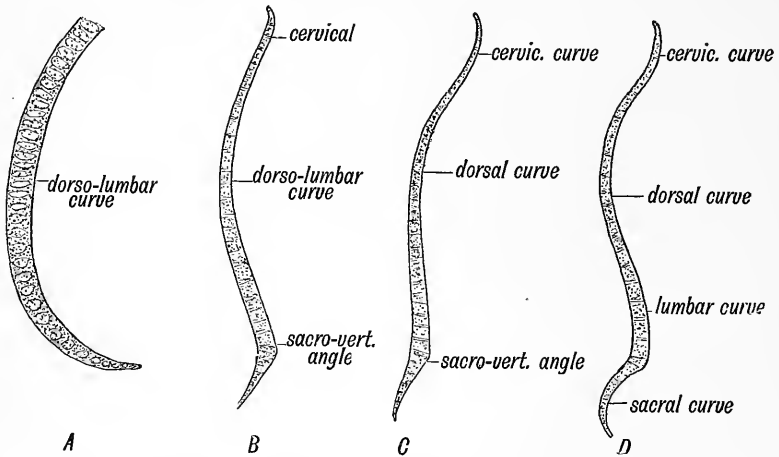


FIG. 48.—Diagram of the Curves of the Spinal Column.

A. At the 6th week of foetal life. B. At the 4th month of foetal life. C. Curves present at Birth. D. Curves present in the Adult.

are of the same generalized type; at a later stage the vertebra of each body-segment assumes its peculiar form, but it is not uncommon for one vertebra to assume some or all of the characters of the one before it or behind it. These variations represent the normal error in developmental markmanship; if need arises the developmental aim can be altered. Such vertebral variations are frequent, and are often of clinical importance.

I. The sacro-lumbar.—The 25th vertebra in 95 % of people forms the 1st sacral; in 1 % the 24th, and 3 % the 26th. These percentages are

¹ For literature on variations of vertebrae: Bardeleben, *Ergebnisse der Anat.* 1905, vol. 15, p. 119; 1906, vol. 16, p. 141; 1908, vol. 18, p. 71. A. Fischel, *Anat. Hefte*, 1906, vol. 31, p. 459. E. Rosenberg, *Morph. Jahrbuch*, 1907, vol. 36, p. 609. F. Wood Jones, *Journ. Anat. and Physiol.* 1910, vol. 44, p. 377 (Influence of Nerve-plexuses in determining Development of Costal Processes). C. R. Bardeen, *Amer. Journ. Anat.* 1905, vol. 4, p. 163 (Development of Vertebrae). E. Barclay Smith, *Journ. Anat. and Physiol.* 1911, vol. 45, p. 144. T. Manners Smith, *Journ. Anat. and Physiol.* 1909, vol. 43, p. 146. A. F. Le Double, *Bull. et Mem. Soc. d'Anthrop.* 1911, Ser. 6, vol. 2, p. 413 (Lumbar Ribs); p. 428 (Cervical Ribs). F. Wood Jones, *Journ. Anat. and Physiol.* 1911, vol. 45, p. 249 (Cervical Ribs). T. W. Todd, *Journ. Anat. and Physiol.* 1912, vol. 46, p. 244 (Cervical Ribs). J. C. Brash (Anomalous Spines), *Journ. Anat.* 1915, vol. 49, p. 243. M. F. Lucas-Keen, *Journ. Anat.* 1915, vol. 49, p. 336.

drawn from the observations of Paterson, Rosenberg, and others who have made researches on this subject. The vertebral formula is not fixed. Rosenberg's investigations showed (Fig. 49) that it is the 26th vertebra that forms the first of the sacral series in the early embryo; later the 25th throws out great lateral masses, and thus forms a connection with the ilia. Bardeen has not been able to confirm Rosenberg's observations; he found that the vertebra which was to form the first sacral—whether it was the 24th, 25th or 26th in the vertebral series—took on a predominance at its earliest appearance. In the lower primates (monkeys) the 27th forms the 1st sacral; with the evolution of man the 26th, then the 25th underwent sacral modifications, the trunk being correspondingly shortened. The lumbar region of the human spine elongates much more rapidly after birth than either the cervical or dorsal region, in order to form an elongated flexible pillar for the support of the upper part of the

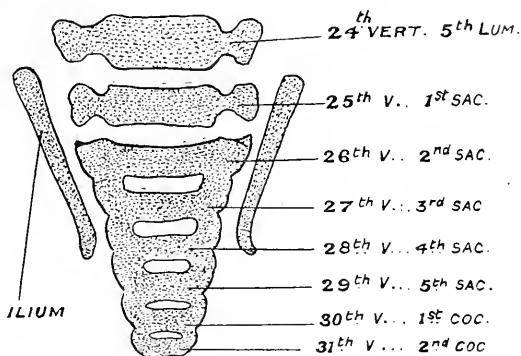


FIG. 49.—A Section of the Lumbo-sacral Region of the Spine in a Foetus at the end of the 2nd month, showing the 26th vertebra forming the 1st Sacral. (After Rosenberg.)

body. In the anthropoid apes the lumbar region is relatively short as in the child at birth. It will be seen that the number of lumbar vertebrae in man is not definitely fixed. The anterior point of attachment of the ilium fluctuates from the 24th to the 26th vertebra. With the sacral transformation of the 25th and 26th (lumbar) vertebrae, there is a corresponding movement forwards of the sacral plexus.

II. **Sacro-coccygeal.**—The 30th vertebra forms the 1st coccygeal; not uncommonly this vertebra is sacral in type and forms part of the sacrum. On the anterior or pelvic aspect of the 1st coccygeal vertebra a rudiment of the **haemal arch** is usually to be found during foetal life. The haemal arches are well developed on the proximal caudal vertebrae of tailed monkeys, and represent developments from the hypochordal or intercentral element of a vertebra. Variations at the distal end of the coccyx are dealt with later (p. 65).

III. **Dorso-lumbar region.**—This region is also liable to variation; the 20th vertebra instead of forming the 1st lumbar, may simulate the 1st dorsal in the type of its articular processes, and may bear ribs, probably

a reversion to an ancestral condition, or, on the other hand, the 12th dorsal vertebra (19th) may not carry ribs. About 2 % of bodies show the latter kind of variation—a reduction of the costal series, and about 6 to 8 % the former kind, in which the costal series is increased (see also Chap. XIX.).

IV. Dorso-cervical.—The 7th vertebra may carry ribs; rarely the 8th vertebra has no ribs attached to it and is cervical in type.

In Fig. 50 is represented the condition of the seventh cervical vertebra, as seen in 72 human skeletons. In the foetus, the costal element is always apparent; in the adult it may vanish or fuse with the transverse process. In about 1 % of individuals it assumes the development shown in Fig. 50, *E*; it may, in occasional cases, assume all the characters of a first dorsal rib, with its anterior end implanted on the presternum. Recently Prof. Wingate Todd has published a series of observations, which are

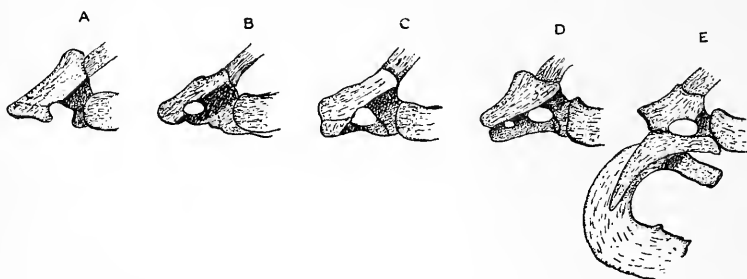


FIG. 50.—Diagram showing the variation in the development of the costal element of the seventh Cervical Vertebra in 72 skeletons. In *A* and *B* the costal element is partly fused with the transverse process; in *C*, *D* and *E* it remains free.

confirmed by the statements made here. A cervical rib may fuse with the costal element of the first dorsal vertebra, thus giving rise to a **bicipital** rib (Dr. Wood Jones). The lower trunk of the brachial plexus crosses a **cervical rib**, and hence in such cases symptoms of nerve-pressure may arise.

V. Cervico-occipital Region.¹—The occipital or posterior part of the skull represents three united vertebrae. Very rarely the last of these may partly assume a vertebral form, but it is by no means rare to see the atlas or first cervical vertebra partly fused with the occipital bone, representing a tendency to add a fourth vertebra to the occipital series.

The Notochord.—In its primitive form, this predecessor of the vertebral column is well seen during the larval stage of certain fishes (Fig. 40, *A*). Its manner of origin in the human embryo has been mentioned already (p. 36). The notochord when first laid down under the neural plate of the embryo is hollow—the hinder end of the canal opening at first at the neurenteric canal. Later the notochordal tube is produced in the primitive streak and later still at the growing point of the tail (Fig. 63). Afterwards

¹ For reports of cases of fusion of atlas: Schumacher, *Anat. Anz.* 1907, vol. 31, p. 145 (Homologies of Occipital Bone); K. Weigner, *Anat. Hefte*, 1911, vol. 45, p. 81 (Assimilation of Atlas); Glaesmer, *Anat. Anz.* 1910, vol. 36, p. 129; Le Double, *Bull. et Mem. Anat.* 1912, p. 20; G. Elliot Smith, *Brit. Med. Journ.* 1908, 2, p. 594; R. J. Gladstone, *Journ. Anat.* 1915, vol. 49, p. 190.

the notochord becomes a solid rod composed of cells of a peculiar type. A sheath is formed round it by cells of the paraxial mesoblast (Fig. 51),

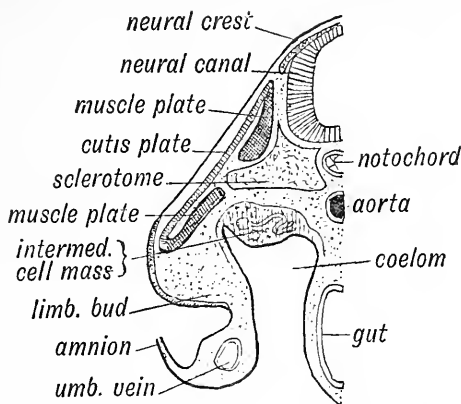


FIG. 51.—A Schematic Section of an Embryo to show the sclerotome, muscle plate and skin plate which arise from each segment of the paraxial mesoblast. (Compare with Fig. 65, p. 67.)

which grow inwards and surround it. These cells form the **sclerotome** and spring from the inner parts of the primitive segments or somite into which the paraxial mesoblast is divided (p. 51).

At the same time the cells of the sclerotome also grow up and gradually surround the neural tube. From these cells which grow inwards and surround the notochord and neural canal, the membranous basis of the spinal column is formed and also the basi-sphenoid and part of the basi-occipital bones of the skull (Fig. 52).

What becomes of the Notochord.¹

In the second month of foetal life the notochord begins to disappear; the bodies of the vertebrae and parachordal cartilages form round its sheath and constrict it. The parachordal cartilages are transformed into the basi-occipital and part of the basi-sphenoid—the basal part of the skull—behind the pituitary fossa. The notochord disappears in the basilar cartilage of the skull. Eternod, however, found the anterior part of the notochord on the dorsal wall of the

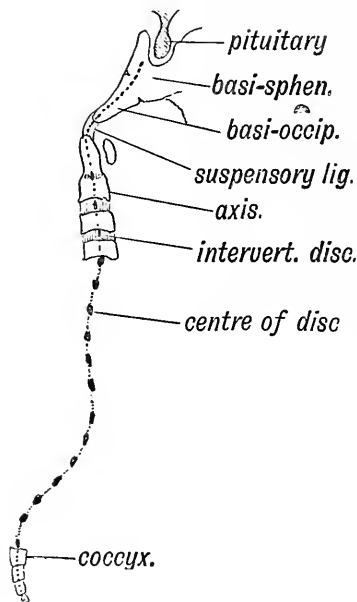


FIG. 52.—Where remnants of the Notochord may occur in the Adult.

¹ Papers on notochord: A. Bruni, *Anat. Hefte*, 1912, vol. 45, p. 307 (Involution of Notochord); A. Linek, *Anat. Hefte*, 1911, vol. 42, p. 607 (Dev. of Notochord); L. W. Williams, *Amer. Journ. Anat.* 1908, vol. 8, p. 251.

pharynx in the human embryo; Robinson has shown that in man the parachordal cartilages are developed in part on its dorsal aspect (Fig. 53). The odontoid process represents the body of the atlas, and the suspensory ligament the disc between the occipital bone and atlas. A remnant of the notochord is enclosed in the suspensory ligament. The centrum or body of each vertebra is formed round the notochord (Fig. 56, *F*), but only between the centra, where the intervertebral discs are formed, does this primitive structure persist. In the discs the notochord swells out and forms a considerable part of the central mucoid core which each disc contains.

Primitive Segments or Somites.—Somites, or protovertebrae as they were formerly named, are not the forerunners of the vertebrae; they are

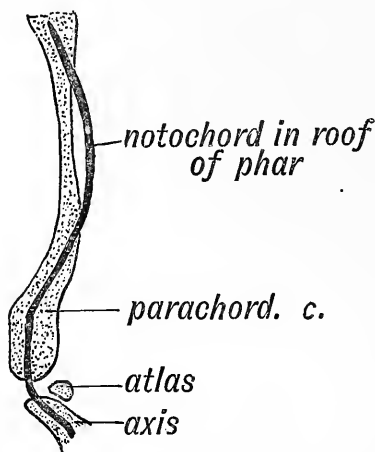


FIG. 53.—The relationship of the Notochord to the basilar or parachordal cartilage of the human embryo. (Arthur Robinson.)

the primitive segments into which the mass of mesoderm at each side of the neural canal and notochord divides (Fig. 51, also Fig. 19). The process of division or segmentation begins at the occipital region towards the end of the third week, and spreads backwards until 35 or more body segments or somites are isolated. Each segment thus separated forms its own muscles (from its muscle plate or myotome), has its own nerve (spinal nerve), its own artery (intercostal), its own cutis plate or dermatome, and the basis for its skeletal tissue (sclerotome) (Fig. 51). The **intersegmental septum** separates one somite from another. Ribs, transverse and spinous processes, are formed in the intersegmental septa. Hence an intercostal space with its muscles, vessels, and nerves, with the corresponding intervertebral structures, represents a differentiated somite. In the ventral aspect of the neck and loins, some of the intersegmental septa disappear.

Morphological Parts of a Vertebra.—The constituent parts of a vertebra, although much modified, may be best recognized in the atlas (see Fig. 54). These parts are (1) the **centrum**, which forms the odontoid

process; (2) the right and (3) the left half of the **neural arch**; (4) the **hypochordal part**, which forms the anterior arch or bow. Besides the four chief elements there are three secondary processes or levers, all of which spring from the neural arch. These are (a) spinous, (b) transverse, (c)

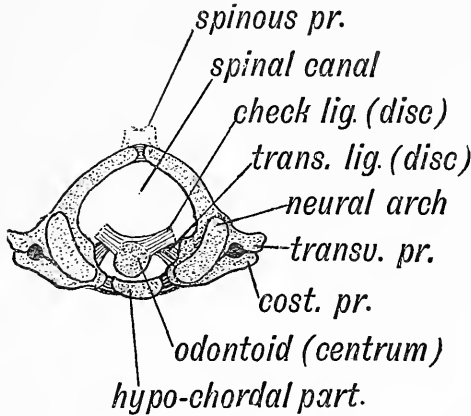


FIG. 54.—The Morphological Parts of the first Cervical Vertebra.

costal processes. In the dorsal region the costal processes become separated from the neural arches by articulations; in other vertebrae they retain their continuity with the arch.

Development of a Typical Vertebra—the 6th Dorsal.¹—(1) **Membranous Stage** (5th and 6th weeks). The vertebra then consists

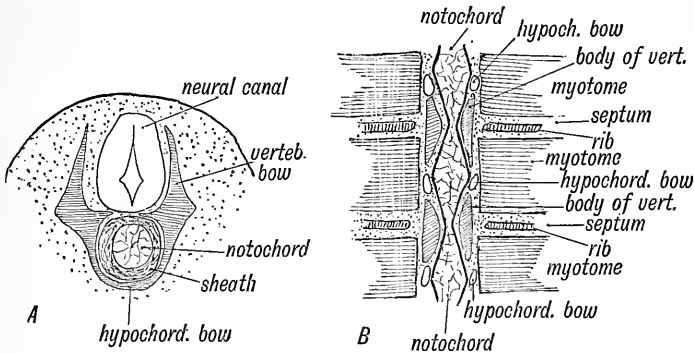


FIG. 55.—The development of the Membranous Basis of a Vertebra.

A. In transverse section. B. In horizontal section showing the relation of the vertebra to the Primitive Segments. The section is viewed from the dorsal aspect.

of 1st a centrum surrounding the notochord, formed from its sheath (Fig. 55, A), and 2nd a horse-shoe shaped **vertebral bow** (Fig. 55, A and B). The bow consists of the right and left limbs which become corresponding

¹ For an account of the differentiation and development of vertebrae: C. R. Bardeen, *Amer. Journ. Anat.*, 1905, vol. 4, p. 163 (Thoracic Vertebrae); also p. 265; 1908, vol. 8, p. 181 (Cervical and Occipital Regions).

parts of the neural vertebral arch and the hypochordal bow which unites the neural arch limbs ventral to the centrum.

(2) **Cartilaginous Stage** (Fig. 56) commences in the 6th week when the embryo is 9 to 10 mm. in length. The fibrous basis of the whole vertebra is transformed into cartilage. In each lateral half of the cellular basis of a vertebra three centres of chondrification appear—one for the neural arch, one for the costal process, and one for each half of the centrum, but those of the centrum soon fuse. In the process of chondrification the cells derived from the sclerotome are directly transformed into cartilage cells. In the atlas the hypochordal part of the bow becomes cartilaginous and subsequently ossified; in all the other vertebrae, excepting the cervical

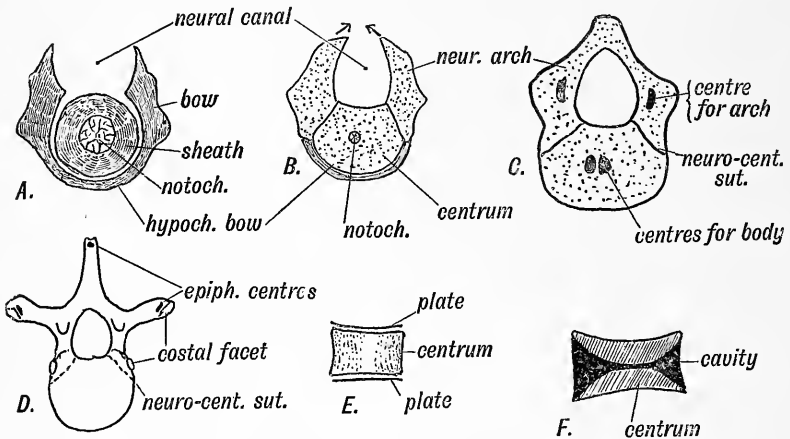


FIG. 56.—Showing the Stages in the Development of a Vertebra.

- A. In the Membranous Stage. B. In the Cartilaginous Stage. C. The appearance of Ossific Points. D. The appearance of Secondary Ossific Centres. E. The epiphyseal plates of the centra. F. Section of an amphicoelous vertebra.

segments just behind the atlas (Fig. 58), this element never passes beyond the membranous stage of development. It should be noticed (Fig. 55, B) that the vertebral bodies are formed round the notochord, *opposite* each intersegmental septum. Hence each centrum must be regarded as the product of two somites. The intervertebral disc is situated opposite the middle of a segment (Ebner). The lateral limbs of the cartilaginous bow meet behind (dorsal to) the neural canal in the 4th month, thus completing the neural arch. At the site of a spina bifida (see p. 83) this union fails.

(3) **Bony Stage.**—The centrum and neural arch elements of the cartilaginous vertebra fuse and give rise to the condition shown in Fig. 56, C. In the 7th week two centres of ossification appear in the centrum, but quickly fuse; one appears in each limb of the neural arch (8th week); at birth the ossific centres of the centrum and neural arch have met. The central and neural ossifications meet at the neuro-central suture, and unite at the 4th or 5th year, the **body** being formed by, (1) the centrum, (2) basal parts of the neural arch (Figs. 54, 56). The neural ossifications

fuse behind (where the spinous process is produced) in the 1st year. The spinous and transverse processes are formed by outgrowths of cartilage into the septa between the somites or primitive segments, where they serve as levers on which the spinal musculature acts. The ribs are also formed by outgrowths from the vertebrae. In the cervical, lumbar and sacral regions they fuse with the transverse processes, but in the dorsal region they remain as separate elements. In typical ribs the head corresponds to the intervertebral disc, because according to Gadov the rib was originally evolved from an intervertebral element—the inter-central or hypochordal. In atypical ribs—the 1st, 11th and 12th—the head of the rib articulates only with the vertebra behind its own disc. Epiphyseal centres for the ossification of the transverse and spinous processes appear about puberty.

The Bodies of Mammalian Vertebrae are peculiar (1) in the development of an upper and lower epiphyseal plate; (2) in that no trace of the noto-

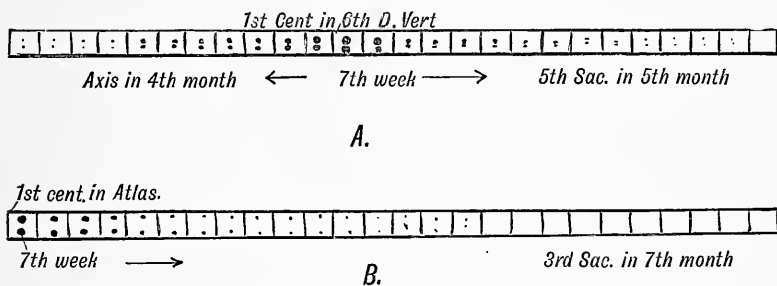


FIG. 57.—The Order in which the Centres of Ossification appear in the Bodies (A) and in the Neural Arches (B) of the Spinal Column.

chord remains within them. In Fishes, as in the early human or mammalian foetus, the bodies are hour-glass shaped (amphicoelous, Fig. 56, *F*); in Amphibians they may retain a concavity in front (procoelous) or behind (opisthocelous), but in mammals both ends are filled up.

It will be observed (Fig. 57, *B*) that the **centres of ossification**¹ for the neural arches appear first in the anterior end of the spine (1st cervical), the date becoming later the more posterior the vertebra. In the 1st sacral they appear about the 4th month; in the 2nd sacral, in the 5th month or later; in the 3rd they may not appear. In the 4th and 5th sacral and 1st coccygeal vertebrae only vestiges of the neural arches are formed. These vertebrae retain the early foetal type shown in Fig. 56, *B*. In the remaining coccygeal vertebrae only the centres for the bodies appear. The centres for ossification of the bodies of the vertebrae appear first in the mid-dorsal region (6th dorsal). From that point they spread forwards and backwards, the centres for the odontoid process appearing at the 4th month, and that for the 5th sacral at the 5th month, while the coccygeal do not appear until about birth.

¹ See F. P. Mall, *Amer. Journ. Anat.* 1906, vol. 5, p. 433 (Centres of Ossification before end of 2nd month); E. Fawcett, *Journ. Anat. and Physiol.* 1911, vol. 45, p. 172 (Costal Epiphyses). Prof. F. Dixon, *Journ. Anat.* 1921, vol. 55, p. 38.

The Atlas and Axis.—The atlas represents the completed bow of the 1st cervical vertebra (Fig. 54). The body of the vertebra fuses with the body of the 2nd, and forms the odontoid process. A remnant of the disc between the 1st and 2nd vertebrae can sometimes be seen when the odontoid is split open. The suspensory and check ligaments are the representatives of the disc between the last occipital segment and the 1st cervical

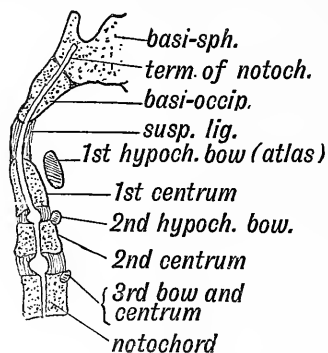


FIG. 58.—A Diagrammatic Section of the Foetal Axis, Atlas, and Basi-occipital.

(Figs. 54 and 58). A nodule in the suspensory ligament may represent an occipital centrum (see p. 144).

Occipito-atlanto-axial Articulations.¹—In the intervertebral discs of the cervical region there is at each side, between the lateral lips of the vertebral bodies, a small articular cavity (Fig. 59). It is situated between the part of the body formed by the neural arches and lies in front of (ventral

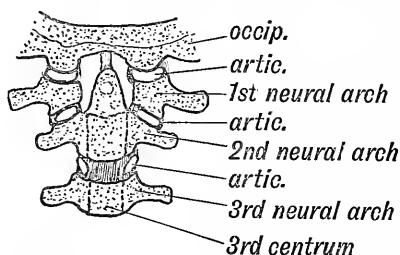


FIG. 59.—The nature of the Atlanto-axio-occipital Articulations.

to) the issuing spinal nerves. Between the axis and atlas this articulation is greatly enlarged. Here the rotatory movements of the atlas on the axis take place. The atlanto-occipital joint, which separates the atlas and the last occipital segment, is of the same nature. The atlas has neither the upper nor the lower articular processes of the other vertebrae. Hence the 1st and 2nd cervical nerves appear to issue behind the articular processes. At one time the single median occipital condyle seen in birds and reptiles was regarded as very different in nature from the double

¹ O. Jaekel, *Anat. Anz.* 1912, vol. 40, p. 609 (Morphology of Atlas).

condyles of mammals. Recently Symington has shown that in the lowest mammals (monotremes), the occipital condyles are fused in the middle line, and that all foetal mammals also show this condition. The articular facets on the upper surface of the atlas are also continuous over the hypochordal element. In the human skull a remnant of this median fusion of the condyles is frequently seen on the anterior margin of the foramen magnum; it is named the third or **median occipital condyle**.

The Ribs are developed as outgrowths of the membranous vertebrae into the septa between the primitive segments of the thoracic region of the embryonic body. In lower vertebrates (birds, reptiles, etc.) each rib has two heads, a dorsal and ventral (Fig. 60). The tuberosity of the human rib represents the dorsal head; the ventral head is well developed in man, as in mammals generally. The rib articulates with the neural arches only (Fig. 56, *D*). The **conjugal ligament** is made up of fibres which cross in the posterior aspect of the intervertebral disc and unite the heads of the

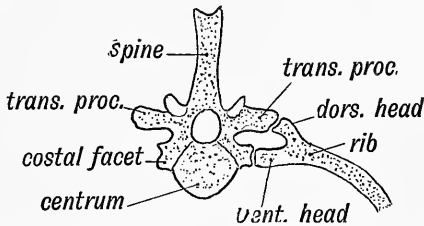


FIG. 60.—The Bicipital Rib of a Lower Vertebrate (crocodile).

corresponding right and left rib. The conjugal ligament which is strong in some animals is weak in man (Bland-Sutton). The transverse ligament of the atlas may belong to the conjugal series.

Vestigial Ribs.—Although the ribs are only fully developed in the dorsal region, yet a representative—a **costal element**—is present in every vertebra. In the **cervical vertebrae** (Fig. 54) the anterior part of the transverse processes represents a costal process, but only in the 6th (sometimes) and 7th is the costal process formed by a separate centre of ossification. The costal process of the 7th, usually represented by a mere vestige, may develop into a rudimentary or even a fully formed rib which reaches the sternum. In the **lumbar vertebrae** only the first shows a separate centre for the formation of the costal process; it fuses with the transverse process in the later months of foetal life; in the other lumbar vertebrae the tips or perhaps the whole of the transverse processes represent costal processes. The 12th dorsal rib varies greatly in size; it may be six or ten inches long or reduced to a mere vestige. In quite 40% of women the 12th rib cannot be palpated because it does not project beyond the outer border of the erector spinae.

In the **1st, 2nd and 3rd sacral vertebrae** the costal processes are large and have their own centres of ossification.¹ Their cartilaginous bases

¹ References to papers on sacrum: E. Fawcett, *Anat. Anz.* 1907, vol. 30, p. 414 (Sacral Costal Epiphyses); Otto Petersen, *Anat. Anz.* 1905, vol. 26, p. 521; D. E. Derry, *Journ. Anat. and Physiol.* 1911, vol. 45, p. 202 (Sacral Accessory Articulations) L. Bolk, *Anat. Anz.* 1912, vol. 41, p. 54.

fuse early to form the greater part of the lateral masses of the sacrum. The part of the lateral mass formed by the costal processes is shown in Fig. 62. The costal processes are absent in the 4th and 5th sacral and in all the coccygeal vertebrae. The two lateral epiphyseal plates on each side of the sacrum are new and independent formations.

The Accessory Processes are found in the lumbar and lowest two dorsal vertebrae. They are developed at the base of the transverse processes and are for the attachment of slips of the longissimus dorsi. The **mammillary processes** are developed on the articular processes of the lower two or three dorsal and all the lumbar vertebrae. They give attachment to tendons of origin of the multifidus spinae. In a paper (*Journ. Anat. and Physiol.*

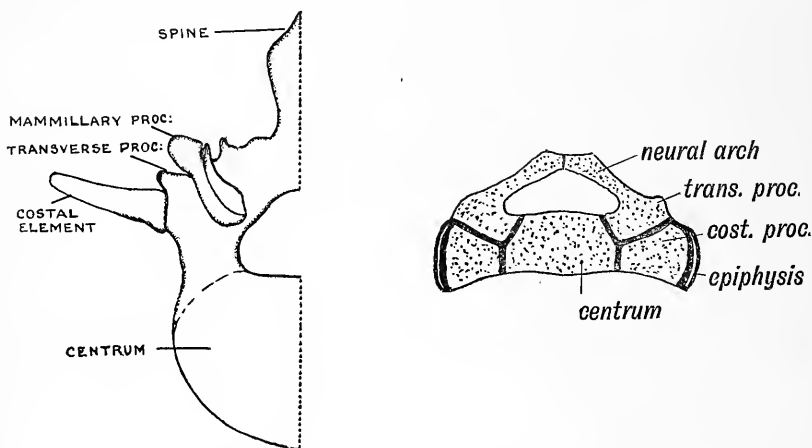


FIG. 61.—Half of a first Lumbar Vertebra showing a separate costal element.

FIG. 62.—A Section to show the Nature of the Elements composing the Sacrum.

1912, vol. 47, p. 118) by Dr. Wood Jones, it is pointed out that these two muscular processes, the mammillary and accessory, are fused together in the dorsal region, but in the lumbar region they are separated by a groove containing the inner branch of the posterior division of the corresponding spinal nerve.

The Transverse and Spinous Processes grow out from the vertebral bow (Fig. 56, A) into the septa between the primitive segments. Each transverse process is pierced, while still in the fibrous condition, by a branch of the corresponding segmental (intercostal) artery. In only the cervical region do those perforating arteries and their foramina persist. In that region the perforating arteries anastomose, and out of the chain thus formed is developed the vertebral artery. Thus the foramina for the vertebral artery are formed independently of the costal element in each cervical transverse process. The spines are absent on the 1st cervical, 4th and 5th sacral and coccygeal vertebrae. They are slightly developed and united by ossification of the interspinous ligament in the 2nd and 3rd sacral vertebrae. The 2nd, 3rd, 4th, 5th, and 6th cervical spines are

bifid in Europeans ; but in lower races, as in anthropoids, the 5th and 6th spines are usually undivided.

Caudal or Coccygeal Vertebrae.—At the end of the 6th week, the body of the embryo being then 11 mm. in length, the human tail reaches its maximum growth—projecting as a conical process fully 1 mm. in length and equal to about one-tenth of the long diameter of the embryonic body. In the adult body the 30th vertebra is usually the first of the coccygeal series. In the fifth week the growing caudal point, at which neural canal,

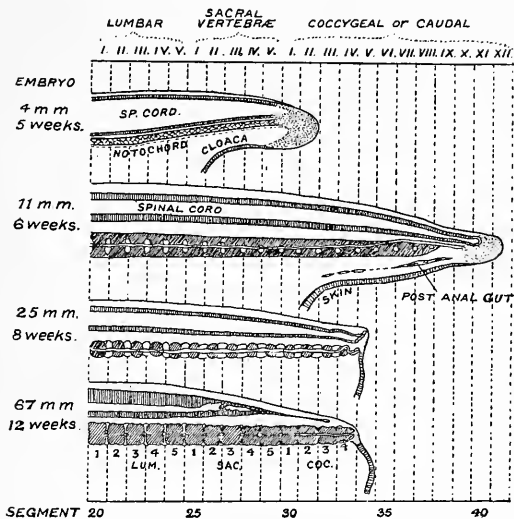


FIG. 63.—A series of four figures showing the condition of the human caudal or coccygeal region at the stages indicated on the drawings (after Kunitomo).

notochord, sclerotomes, and cloaca are all being extended in a backward direction, has reached and produced the 30th segment (Fig. 63); at the 6th week, ten or twelve caudal segments have been laid down. Thereafter retrogression sets in; by the end of the 8th week (Fig. 63) only the caudal tip projects and the coccygeal vertebrae have been reduced to 4 or 5, while, by the 13th week, a depression or pit marks the site where the tip disappeared. The coccygeal part of the neural canal is atrophied and the distal part of the whole cord is retracting in a cranial direction.¹

¹ See Prof. G. L. Streeter, *Amer. Journ. Anat.* 1919, vol. 25, p. 1; Dr. Kanae Kunitomo, *Contrib. to Embryology*, 1918, vol. 8, p. 161.

CHAPTER VI.

THE SEGMENTATION OF THE BODY.

At the end of the 3rd week, as we have already seen (p. 18), the paraxial mesoderm, lying at each side of the neural tube, becomes divided from before backwards into somites or primitive segments, their demarcation becoming evident first in the occipito-cervical region of the body. By the end of the 4th week the process has reached the 1st coccygeal segment, there being then 3 occipital and 30 body somites. The occipital somites disappear prematurely but those of the body, although they become specialized and broken up, can still be recognized in the adult. In the

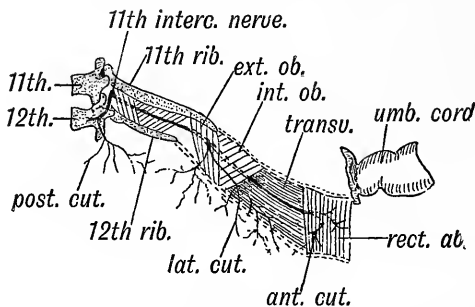


FIG. 64.—Some of the structures derived from the 11th Dorsal Segment of the Right Side.

preoccipital region of the head, parts are also arranged on a segmental plan, one which is older than the vertebrate segmentation of the trunk and can best be identified by the visceral or gill arch system of the pharynx.

Segmentation of the Body.¹—The human body or trunk consists of 33 or 34 segments. Each segment is fundamentally of the same type, but the resemblance is obscured owing to extensive modifications which the somites undergo to form the cervical, dorsal (thoracic), lumbar (abdominal), sacral (pelvic) and caudal regions of the body. The outgrowth of the limbs also renders it difficult to recognize in the adult the simple system of segments which can be seen in the embryo at the end of the third week (Fig. 19, p. 17).

¹ For papers on segmentation see: G. van Rynberk, *Ergebnisse der Anat.* 1908, vol. 18, p. 353; A. L. J. Sunier, *Onderzoekingen verricht in het Zoolog. Lab. Univ. Groningen*, 1911, Leyden (Differentiation of Myotome). See also references:—Bar leen, p. 54; under W. H. Lewis, p. 426; Watt, p. 42; Barnville, p. 47.

Until lately the segmentation of the human body was a matter of only speculative importance, but recent advances in our knowledge of the distribution of nerves have shown that it has a direct bearing on diagnosis and treatment.

Constitution of a Typical Segment (11th Dorsal).—It is better to study the development of a typical body segment, and from that the student will be able to note for himself the modifications which have taken place in the more highly differentiated segments of the body. As already explained, the process of segmentation affects chiefly the paraxial block of mesoderm which lies on each side of the neural canal and notochord,

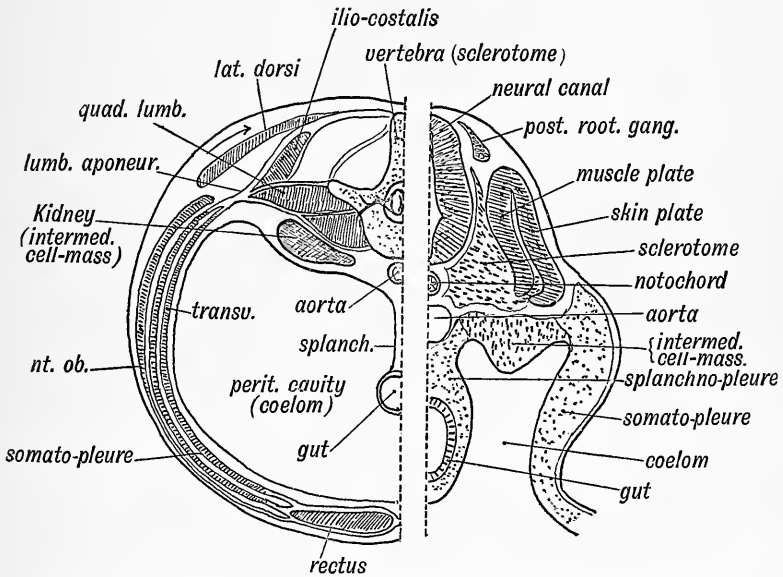


FIG. 65, A.—A Transverse Section showing the Elements of the 1st Lumbar Segment in the Adult.

B.—A corresponding Section of an Embryo about the end of the 4th week (diagrammatic).

and also, to a lesser degree, the intermediate cell mass. In Figs. 65, *A*, *B*, a body-segment is represented in the adult and in the embryonic condition.

The following elements make up the 11th dorsal segment: (1) Its skeletal basis; (2) Muscular element; (3) Renal element; (4) Vessels; (5) Nerves; (6) Neural segment; (7) Cutis plate. Although the ectoderm and entoderm are never segmented, yet a definite area of each is associated with every body segment. The origin of each element will be taken separately.

I. The **skeleton** of the 11th dorsal segment is represented by the adjacent halves of the 11-12 dorsal vertebrae and the disc between them, for, as already pointed out, the vertebrae are intersegmental in their development (Fig. 55, *B*). The transverse processes, the spinous processes and 11th and 12th ribs are also formed in the septa in front of and behind the 11th

segment (Fig. 64). The septum in the rectus muscle a little below the umbilicus represents the intersegmental septum corresponding to the 11th rib. Sometimes another septum occurs in the rectus, midway between the pubes and umbilicus, marking the lower limit of the 11th segment. The linea alba separates the segments of the two sides.

In the linea alba or ventral median line of the thoracic region, the sternum is developed. The intersegmental septa are well marked in the thoracic region; the ribs and their cartilages are developed in them. In the neck the septa are almost lost; the intermediate tendon of the omo-hyoid and the septa occasionally found in the sterno-hyoid and -thyroid, complexus and trachelomastoid muscles are the only representatives of them in the cervical region.

II. The Muscles of the 11th Dorsal Segment.—All the muscles of this segment are developed from the muscle plate (myotome) of the primitive segment (see Figs. 64 and 65). There is a cavity, which probably arises as a diverticulum of the coelom, in each primitive segment (Fig. 39, p. 39). The cells of the mesoderm on the inner side of the segmental cavity become columnar and form the muscle plate (Figs. 51, 64). Each segment has its own muscle plate. The cells or myoblasts of each plate increase rapidly in number, forming a fused mass or syncytium;¹ they spread into the somatopleure, and form the muscles of the body wall and limbs. In the myosyncytium fibrillae and fibres are formed; each fibre becomes elongated and directed across its segment from septum to septum. The intercostal muscles retain this arrangement, but in the abdominal region the fibres fuse with those of neighbouring segments to form muscular sheets—the external oblique, internal oblique, transversalis and rectus. In the foetus of the fifth month traces of these septa may be seen; Bardeen found that the intercostal nerves retained their segmental distribution in the muscles of the belly wall. In fishes the embryonic segmental arrangement of the musculature persists. The manner in which the final groups of muscles are derived from the muscle plates is not accurately known, but in the typical segment with which we are at present dealing it will be seen that the musculature falls into two groups (see Fig. 65, A): (1) **epaxial**, the erector spinae, etc.; and (2) **ventro-lateral** or body-wall muscles (intercostals, rectus, oblique muscles, etc.). The musculature of the limbs is derived from the ventro-lateral group (Figs. 446, p. 423; 455, p. 432).

The ventro-lateral sheet separates into a **ventral longitudinal** band and a lateral transverse-oblique stratum. Each of these divides into an inner and outer **primary** layer; the outer and inner **secondary** layers arise as delaminations of the primary layers, thus making four in all. The internal oblique and transversalis, and internal intercostal are derived from the internal primary layer; the external oblique and external intercostal from the external primary layer.² The rectus abdominis represents the deeper of the two layers derived from the external primary. Parts

¹ See Prof. J. Cameron, *Trans. Roy. Soc. Canada*, 1918, vol. 11, p. 81.

² See Prof. T. Walmsley, *Journ. Anat.* 1916, vol. 50, p. 165.

of the deepest layer of the lateral sheet, represented in the adult by the transversalis, have migrated inwards to form the subvertebral or **hypaxial** muscles—the quadratus lumborum, crura of the diaphragm, longus colli, rectus capitis anticus major and minor, and the levator ani. When muscles migrate they invariably carry with them the nerves of the body segments in which they are developed. Hence the nerve supply affords the clue to the segments from which a muscle or part of a muscle arises. The middle layer of the lumbar fascia is developed between the epaxial and ventrolateral musculatures.

Many of the ventro-lateral muscles (trapezius, rhomboids, and latissimus dorsi), migrate dorsalwards over the epaxial muscles, and take origin from the spines of the vertebrae (Fig. 65, *A*).

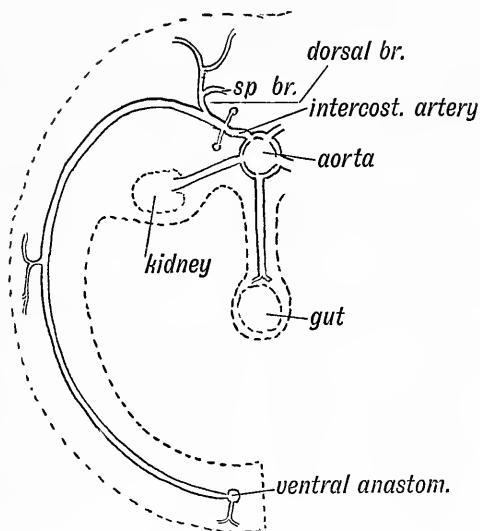


FIG. 66.—The distribution of a typical Segmental Artery.

Muscular fibrillae begin to form in the 5th week, appearing in the protoplasmic matrix, in which the nuclei of the **myoblasts** are embedded. The fibrillae group themselves in bundles or muscle fibres, the nuclei with some of the myoplasm being applied to the surface of the completed fibre. New fibre production goes on rapidly until the 5th month, when the complement for each muscle is nearly complete. Thereafter muscles grow in size, chiefly, it is believed, by an increase in the size of the individual fibres. Although voluntary muscle fibres atrophy when their nerve is cut, yet myoblasts will develop into muscles when separated from nerve cells (Ross Harrison), or when grown in artificial media outside the body.

III. **The Arteries of the 11th Segment**¹ (Fig. 66).—The 11th intercostal is the artery of the segment. It gives off a dorsal branch to supply the epaxial muscles, the spinal column, spinal cord and membranes, and skin.

¹ For segmentation origin of arteries see : I. Broman, *Ergebnisse der Anat.* 1906, vol. 16, p. 639.

The segmental artery joins at its termination with a ventral longitudinal vessel, the deep epigastric. The primitive arrangement in vertebrates appears to have been one with a dorsal and ventral longitudinal vessel, the segmental artery passing from the dorsal to the ventral vessel. The vertebral, ascending cervical, deep cervical, ascending lumbar and lateral sacral arteries are examples of the anastomoses that may arise between segmental arteries.

Segmental arteries also arise from the aorta to supply the structures formed from the intermediate cell mass (the kidney, testis, ovary, etc., Fig. 66). As a rule only one renal segmental artery persists, but frequently accessory renals are seen. These may be persistent embryonic vessels of several segments of the intermediate cell-mass in which the Wolffian body and kidney arise. The splanchnopleure shows no certain traces of segmentation; hence its vessels (coeliac axis and mesenteric) if of segmental origin have become profoundly modified. Lately Broman has demonstrated that the splanchnic arteries have the appearance of a segmental arrangement in the embryo (Fig. 25). During the 4th week there are right and left aortae, each giving off splanchnic branches; in the 5th week fusion of the aortic trunks sets in; later the right and left splanchnic branches unite.

IV. The Nerve Elements of the 11th Segment (Fig. 67).—Although the spinal cord during development of the human embryo shows no clear sign of being definitely divided into segments corresponding to those of the body, yet from what we know of its condition in embryos of other animals and from clinical evidence there can be little doubt that such a segmentation does take place, and that it possesses segments corresponding to those of the body. From each segment four groups of cells arise: (1) Somatic motor, (2) somatic sensory, (3) splanchnic motor, (4) splanchnic sensory. The motor groups for the greater part remain within the spinal cord, but many enter the sympathetic ganglia; the sensory groups form ganglia outside the cord. The nerve fibres connected with the somatic groups have a diameter varying from $9-18\mu$; those with the splanchnic, $2-9\mu$. The **somatic motor** group, in the anterior horn, sends out processes to all the muscles of the primitive body segment in which it is situated. The anterior root of a spinal nerve is formed by the somatic motor fibres. The **splanchnic motor** cells, in the lateral horn, send out processes within the splanchnopleure which reach viscera through the white rami communicantes and sympathetic system (Fig. 67, *A*). It is probable that, as Elliot Smith has suggested, some of the splanchnic motor cells emigrate from the cord and take up a position in the prevertebral ganglia.

At the point where the medullary plates are cut off from the ectoderm to form the neural canal, a crest, **the neural crest**, grows out on each side (Fig. 67, *B*) composed of the cells which formed the junctional line between medullary plates and ectoderm. A group of these neuroblasts—the **somatic sensory** group—grows into each segment and forms the **posterior root ganglion**. Each neuroblast within the ganglion sends out a process which bifurcates, one branch or fibre growing into the cord and ending in the posterior column and cells of the posterior horn, the other passing

to the skin, muscles, etc., of the segment. The posterior nerve root is thus formed by the ingrowing processes from the cells of the posterior root ganglion, and the body segment in which the outgrowing processes are distributed is thereby brought into sensory communication with the central nervous system (see also p. 84). The anterior and posterior roots unite to form a spinal or segmental nerve. Like the artery, it divides into a posterior division for the epaxial part of the segment and an anterior for the ventro-lateral part (Fig. 67, *A*). The **splanchnic sensory**¹ groups are situated in the posterior root-ganglia, and probably also in the various ganglionic masses of the sympathetic system. These sympathetic cells are derived, with the posterior root ganglion, from the neural crest, and at

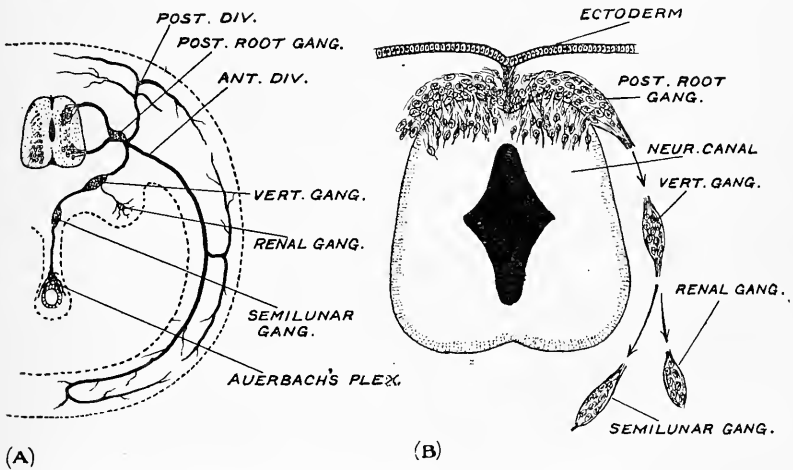


FIG. 67. *A*.—Diagram of the Nerve System of the 11th Dorsal Segment.

B.—A diagram showing the derivation of the Parts of the Nerve System of the 11th Segment in the Embryo.

first form a continuous paravertebral column (in 5th week). From the paravertebral column are differentiated :

(a) The prevertebral ganglion situated on the vertebra (in the gangliated chain), ventral to the exit of the spinal nerve ;

(b) A group to the intermediate cell mass (renal ganglion and adrenal body) ;

(c) Another to the splanchnopleure (in the semilunar ganglia) ;

(d) To the viscera (cells of Auerbach's plexus, etc.).

Groups (c) and (d) show no trace of segmentation in their arrangement, but, clinically, evidence is to be found that every viscus or part of a viscus is connected with certain segments of the spinal cord. The cells of the sympathetic ganglia throw out axis-cylinder processes, which are connected with the spinal cord by fibres in a white ramus communicans and posterior root, and act as sensory pathways from the viscera. The distal end of the axis-cylinder process terminates in a viscus. In this manner certain segments of the spinal cord are brought into touch with certain parts of

¹ See Gaskell's original paper in *Journ. of Physiol.* 1886, vol. 7, p. 1.

the viscera. The vaso-motor supply of each body segment passes to it from the sympathetic ganglion by a grey ramus communicans.

It will thus be seen that all the parts of a segment—body wall (somatopleure), kidney (intermediate cell mass), and a part of the abdominal or thoracic viscera (splanchnopleure) are connected by nerves to a corresponding segment of the spinal cord. In diseased conditions of any part of a body segment, the corresponding spinal segment of the cord is disturbed. Such a disturbance is referred along the somatic sensory fibres, for the brain has no power to assign to their source, impressions travelling inwards by the splanchnic sensory fibres. Thus, for instance, a stone in the pelvis of the kidney (which is supplied from the 10th, 11th, and 12th dorsal segments) is frequently accompanied by pain which the brain refers along the 11th and 12th intercostal nerves. The skin supplied by these nerves

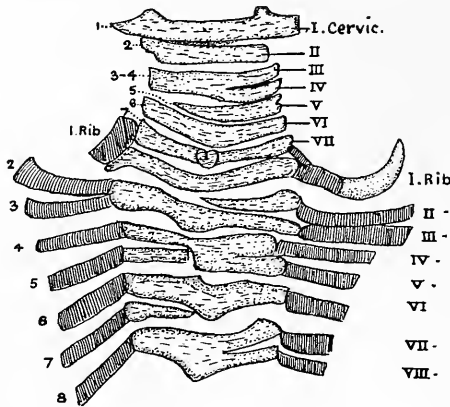


FIG. 68.—Cervical and dorsal parts of the Spine of a Human Foetus showing irregularities of segmentation.

may become hyper-aesthetic. In the central nerve system as in the muscular, the primary simple segmental arrangement has been disturbed by enormous changes which have occurred in the process of evolution. In order to secure a harmonious co-operation of the various segments of the body, communications have been established, by means of nerve tracts, between the various segments of the spinal cord and between the segments of the cord and the higher centres of the brain. These communications have obliterated well nigh all traces of the primitive segments, and yet we see in the ganglia of the posterior roots and in the prevertebral ganglia of the sympathetic chain clear evidence that each segment of the body was originally provided with its own semi-automatic nerve mechanism. Clinical observation has supplied evidence that certain viscera—such as the heart, the liver, the kidneys—have a nervous correlation with certain segments of the body, and we may infer that these organs have been evolved in connection with certain definite segments of the body.

Segments from which Splanchnic Fibres Escape.—The small medullated or splanchnic fibres do not arise from every spinal segment.

Bishop Harman found that in man such fibres escape only by the roots of the dorsal nerves and first lumbar ; occasionally splanchnic fibres come out in the roots of the last cervical and second lumbar. These fibres enter the gangliated chain, and are distributed to the viscera. Splanchnic fibres also escape by the 3rd sacral, frequently too from the 2nd or 4th, to form the *nervi erigentes* for the pelvic viscera. The greater part of the 9th, 10th and 11th cranial nerves is made up of splanchnic fibres. There are thus three visceral areas—an anterior or medullary, a middle or thoracic, and a posterior or sacral. How these centres came to be thus separated is not known. It is also remarkable that the nerve centres which regulate or constrict arterioles are situated in the middle or thoracic area.

Abnormal Segmentation.—In certain pathological conditions the process of segmentation is disturbed, with the result that an irregular and asymmetrical separation of the segments takes place. In Fig. 68 part of the spinal column and ribs are shown of a foetus in which the effects of such an irregularity are well illustrated. The vertebrae of the 3rd and 4th cervical segments are fused on the left side ; the succeeding segments show many abnormalities of a similar kind. The bodies of the 1st and 2nd ribs of the right side are fused. In the same foetus the pectoral muscles were imperfectly developed. In such foetuses one or both of the shoulders are placed high in the neck (**congenital elevation of the scapula**). Imperfect separation of two adjacent vertebrae or ribs is occasionally seen—abnormalities due to a lesser irregularity of segmentation.

CHAPTER VII.

CENTRAL NERVOUS SYSTEM—DIFFERENTIATION OF THE SPINAL CORD.

Evolution of the Central Nervous System.—To students who are familiar with the extraordinary complexity of the central nervous system of man it must seem incredible that it arose by the specialization of an area of the ectoderm or covering of the body. It is only on such a hypothesis that we can explain the fact that the medullary plates, out of which the whole central nervous system of the body is developed, are exposed on the surface of the embryo during the greater part of the 3rd week of development. It occasionally happens that children are born, in which

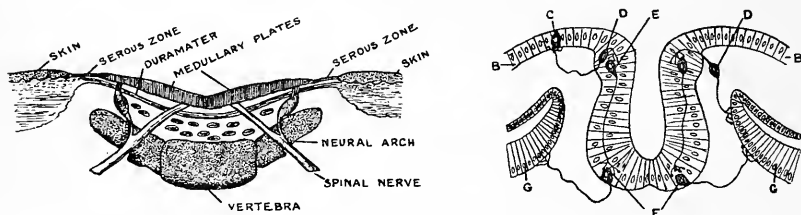


FIG. 69.—Diagrammatic Section across the Back of an Anencephalic Child in which the medullary plates were exposed on both head and spine.

FIG. 70.—Diagram to show how the ectodermal cells of the Medullary Plates are differentiated into nerve cells or neuroblasts and supporting cells or spongioblasts. (After Prenant.) The central canal is being enclosed by upgrowth of the medullary plates. *B, B*, ectoderm; *C*, sensory cell in ectoderm; *D, D*, cells which become enclosed in posterior root ganglion; *E, E*, nerve cells which connect the sensory and motor cells; *F, F*, motor cells in anterior horn; *G, G*, muscle plates.

the medullary plates are exposed along the head and back as they are during very early embryonic life. The condition is shown in Fig. 69, and it is impossible to explain its occurrence except by supposing the medullary plates to be modified parts of the ectoderm. When, however, one remembers the condition in the lower invertebrates, such as is seen in the organization of the Hydra, the explanation becomes more acceptable. The ectodermic cells of Hydra are not only protective and secretory in function, but they also serve the purposes of nerve cells and muscle cells. One can understand how a specialization of function in the ectodermal cells may have occurred—some becoming purely contractile, others purely sensory, or secretory, or protective. In the cells of the medullary plate we see a further specialization (see Fig. 70); cells are specialized to connect the sensory with the contractile or muscle cells. Those connected with the

sensory cells—the posterior root ganglia—arise near the lateral margins of the medullary plates; those connected with the muscle cells arise near their mesial margins. If this hypothesis is true, then the central canal is merely an enclosed tube of ectoderm and filled with fluid, because the form of animal in which the medullary plates were evolved was a water-living form. Dr. W. H. Gaskell has advanced the view that the central canal represents a former alimentary tube round which nerve cells have gathered. While Dr. Gaskell's hypothesis explains many facts, it leaves many more unexplained—especially the manner in which the central nervous system is developed.

Formation of the Central Canal.—The medullary plates of ectoderm, which form the spinal cord and brain, rise up, meet, and enclose a canal—the central canal of the spinal cord and brain (Fig. 71). The lips of the

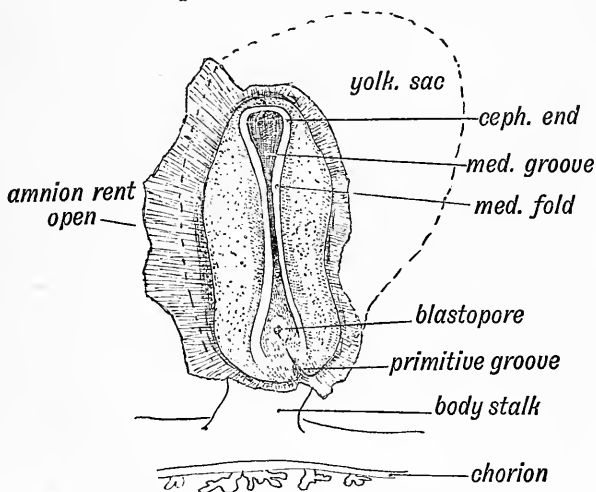


FIG. 71.—Medullary Folds uniting to form the Neural Tube in a Human Embryo in the 3rd week of development. (After Graf Spec.)

medullary plates meet and fuse together in the cervical region first, the process of union spreading forwards and backwards, the last parts to be enclosed being the cephalic and caudal extremities. The opening at the anterior extremity—the **neuropore**—and the posterior or **caudopore** close towards the end of the 4th week, the neuropore closing first. The optic vesicles begin to grow out from the medullary plates before these have united to enclose the cavity of the fore-brain. It will be thus seen that the optic vesicle, which becomes the retina and optic nerve, is developed as a part of the medullary plate.

Division of the Neural Canal (Figs. 72, 73).—At the end of the 4th week the neural tube is divided into four parts. They are :

(1) An anterior dilatation, the fore-brain, which forms the 3rd and lateral ventricles and their walls.

(2) The mid-brain, which becomes transformed into the aqueduct of Sylvius, corpora quadrigemina and crura cerebri.

(3) The hind-brain, the basis of the 4th ventricle, pons, cerebellum and medulla.

(4) The central canal and spinal cord.

The Spinal Cord.—The Spinal Cord at first extends throughout the whole length of the spinal column. At the end of the 3rd month the spinal column and canal grow more rapidly than the cord, and at birth its lower end has become withdrawn to the level of the 3rd lumbar vertebra.¹ By

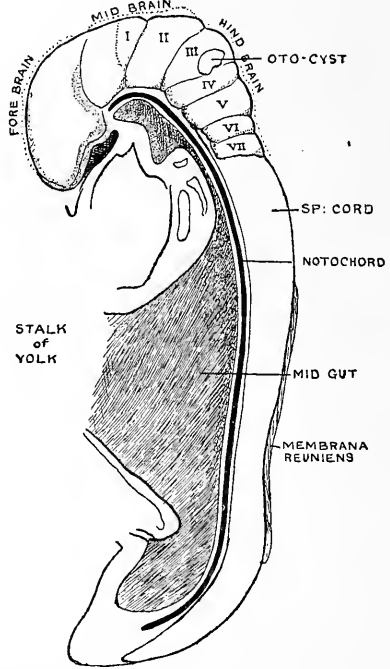
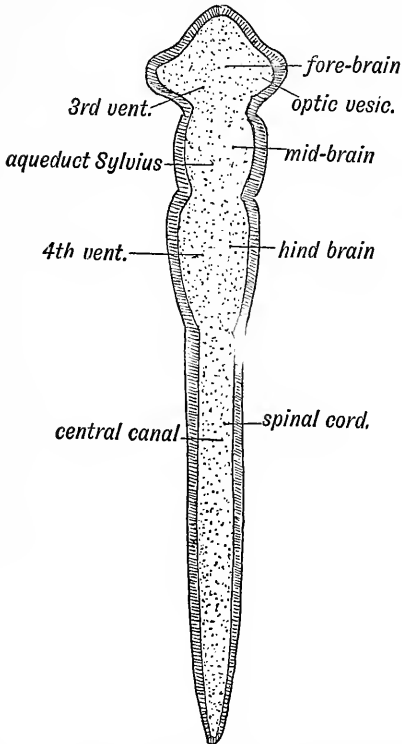


FIG. 72.—Diagram of the Four Primary Divisions of the Neural Tube.

FIG. 73.—Lateral View of the Central Nerve System of a Human Embryo of the 4th week—2.6 mm. long. (Dr. Low.)

the third year it usually terminates opposite the disc between the 1st and 2nd lumbar vertebrae, but it may stop at the lower border of the 2nd lumbar or rise as high as the middle of the 12th dorsal vertebra.² The results of this inequality of growth are :

(1) The roots of the lumbar and sacral nerves become enormously elongated, forming the cauda equina ; all the nerves are more or less drawn up, except the 1st and 2nd cervical ; the origins of the lower cervical nerves are drawn up 2 vertebrae (as indicated by the position of their spines) ; the upper dorsal, 3 ; the lower dorsal, 4 ; the lower lumbar, 5 ;

¹ G. L. Streeter, *Amer. Journ. Anat.* 1919, vol. 25, p. 1.

² R. E. McCotter, *Anat. Rec.* 1916, vol. 10, p. 559.

the coccygeal, 10. These statistics represent a broad expression of the observations made by Professor R. W. Reid.

(2) The **caudal part** of the spinal cord is the last part of the neural tube to be formed (see Fig. 63). Its fate has been recently investigated by Professor Streeter.¹ Even in the 9th week (Fig. 73, A) the caudal segment is still represented over the coccyx, ending in a subcutaneous vesicle, but already retrogression has set in, the coccygeal ganglia have disappeared and the neural canal, immediately distal to the origin of the 5th pair of sacral nerves, is becoming dilated to form the terminal ventricle. By the 12th week (Fig. 74), when retraction has set in, we see that the caudal segment has become differentiated into a distal or extradural part, which

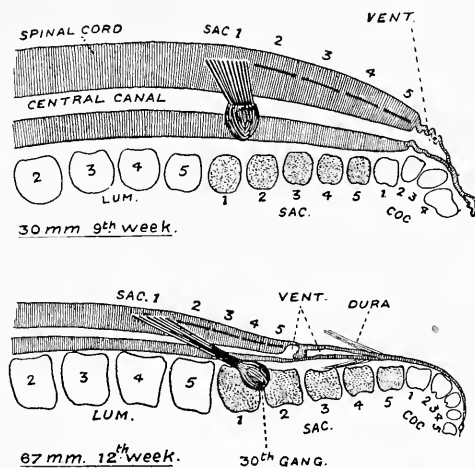


FIG. 73, A.—Showing the differentiation of the terminal part of the neural tube into the coccygeal thread and filum terminale. (Streeter.)

is drawn out to form the coccygeal thread, while the intradural part is being stretched and will become the filum terminale.

Differentiation of the Spinal Cord.—As the neural plate is folded in towards the end of the 3rd week, the single layer of columnar epithelium of which it is composed is already undergoing certain changes. Three stages in its differentiation are shown in Fig. 74; in Stage I., the single layer of ill-defined columnar cells is shown; the bases of the cells are directed towards the central canal, resting on a delicate *internal limiting membrane*; their outer ends, appearing on the surface of the neural tube, are bounded by the *external limiting membrane*. In Stage II. there has been an active proliferation of the cells and an increase in the thickness of the neural wall; the cell bodies have fused to form a cytoplasmic syncytium, in which the nuclei are spread between the inner and outer limiting membrane. In Stage III. (Fig. 74), which is reached about the close of the 4th week, the wall has made a further increase in thickness; in the common cytoplasm a fibrillar meshwork—a **myelospongium**—has been laid down;

¹G. L. Streeter, *Amer. Journ. Anat.* 1919, vol. 25, p. 1.

three zones can be distinguished, a middle or mantle zone in which most of the nuclei are contained, which will become the grey substance of the cord ; an outer or marginal zone made up of myelospongium into which the fibre-tracts of the cord will grow ; an inner or ependymal zone, not

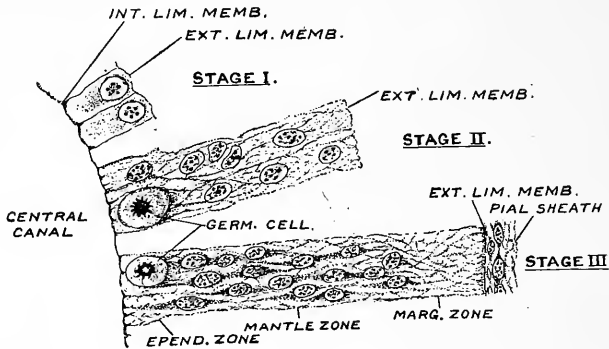


FIG. 74.—Three stages in the early differentiation of the wall of the spinal neural tube. Stage I., single layer of ill-differentiated columnar epithelium ; Stage II., in which the single layer has been transformed into a nucleated syncytium ; Stage III., in which three zones begin to be apparent. (After Streeter.)

distinctly demarcated, but characterized by the presence of actively dividing large nuclei—*germinal cells*. The nuclei, with their surrounding protoplasm, are becoming differentiated into neuroblasts—the producers of nerve cells, and neuroglial or supporting cells. The neuroglial fibres

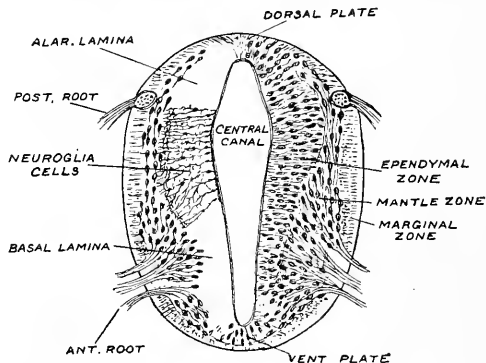
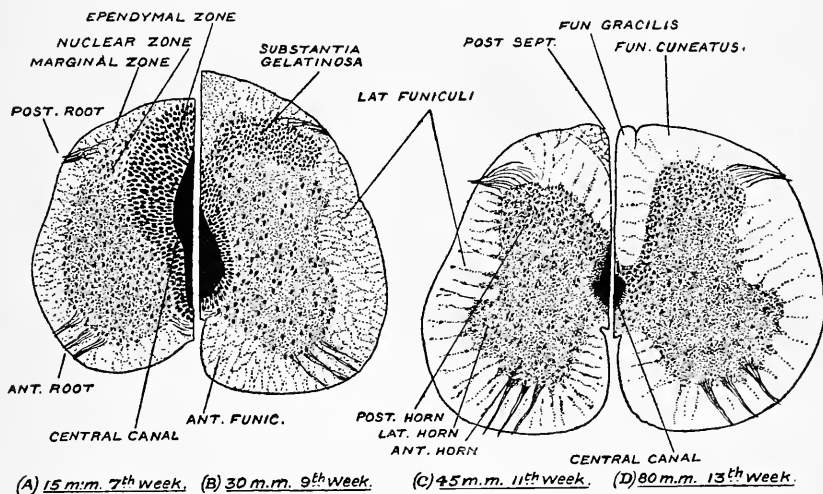


FIG. 75.—Section across the developing Spinal Cord at the beginning of the 5th week. (After His.)

are laid down in the cell-protoplasm of neuroglial cells. The ependymal cells, which line the central canal, are derived from the inner zone.

A section across the embryonic spinal cord at the beginning of the 5th week (Fig. 75) brings out certain instructive features : the central canal is coffin-shaped in section ; the epithelium in its roof and floor—forming the **roof and floor plates**—increases but slightly in thickness ; its side walls, walls, or lateral plates, which become the cord or medulla, are indistinctly

separated into a ventral part or **basal lamina**, from which the anterior root fibres emerge and which will have to do with motor functions and a dorsal part—the **alar lamina**, into which the fibres of the posterior root grow and which will have to do with sensory functions. The three zones in each lateral plate are distinct; the inner or ependymal zone increases in breadth as it is followed from the floor plate to the roof plate, whereas the middle or mantle zone does the opposite; it diminishes as it passes into the alar lamina. In the ventral part of the middle zone the anterior grey column or horn is quite apparent, whereas the posterior horn is just beginning to form. We must suppose that the inner or ependymal zone is one of production or proliferation and that its cells are becoming differentiated and added to the middle zone. The anterior or motor column is demarcated



(A) 15 m.m. 7th week. (B) 30 m.m. 9th week. (C) 45 m.m. 11th week. (D) 80 m.m. 13th week.

FIG. 76.—Showing the progressive differentiation of the spinal cord during the second and third months of development. (After Streeter.)

before the posterior or sensory horn. In each lateral plate the neuroblasts become grouped thus from anterior to posterior horn: (1) somatic motor, (2) splanchnic motor (both in the basal lamina), (3) splanchnic sensory, (4) somatic sensory (both in the alar lamina). This order of grouping holds true from end to end of the neural tube. The fibres from the cells in the anterior horn begin to emerge as the anterior root in the latter part of the 4th week; the processes from the ganglion cells of the posterior root commence to enter the marginal zone of the alar lamina at the same time. As is diagrammatically represented in Fig. 75 neuroglial fibres pass from the lining ependyma of the central canal to the external limiting membrane.

The developmental changes in the cord during the 2nd and 3rd months are set out in a semi-diagrammatic manner in Fig. 76, A, B, C, D. We may centre our attention first on three structures—the central canal, the inner or ependymal zone and the posterior median septum, for all three are closely correlated. In the 7th week (Fig. 76, A) the central canal still

retains its coffin-shaped section, the ependymal zone is still extensive, and although the roof plate has thickened there is still no posterior median septum, for the posterior funiculi or conducting tracts (*f. gracilis* and *f. cuneatus*) have scarcely appeared in the dorsal marginal zone. In the 9th week changes are in progress: the dorsal part of the central canal is being obliterated by the apposition of the lateral plates (Fig. 76, *B*); the ependymal zone is reduced; the posterior funiculi are being formed in the dorsal marginal zone and the posterior-median septum is formed between the right and left posterior funiculi developing on each side of the original roof plate. In the 11th week the central canal and ependymal zone are further reduced; the posterior-median septum has increased in depth owing to the rapid growth of the posterior funiculi; the middle or mantle zone is now differentiated into the anterior and posterior columns of grey matter. In the 13th week the adult condition is reached; the cord is reduced to its final size, the ependymal zone now forms merely a lining to the canal; the anterior and posterior horns, with their various groups of nerve cells, are reaching their final form, while in the marginal zone the great connecting and association tracts of white matter have arisen or are arising. There is now a deep posterior median septum and an open anterior median fissure, formed during the development of the ventral funiculi in the anterior part of the marginal zone.

Spinal Tracts.—With the formation of the posterior columns, the grey matter of the dorsal laminae, at first united by the roof plate, becomes widely separated to form the posterior horns (Fig. 77). At the same time part of the gelatinous tissue of the inner zone is separated to form a cap on the posterior horns (Fig. 76). In the gelatinous tissue congenital cysts may occur. The columnar cells which line the central canal are ciliated. Thus by the end of the 3rd month the nerve cells have taken up their permanent stations in the grey columns of the spinal cord. The cells which have to do with the reception and transmission of sensory messages are situated in the posterior root ganglia; those which have to do with the dispatch of motor impulses are situated in the anterior and lateral horns; the remainder may be regarded as intercalated or shunt cells, and are concerned in linking up or associating the afferent and efferent systems and centres. The marginal zone provides a basis into which the nerve processes—the axons which are to connect neuron with neuron and centre with centre—may grow and reach their destinations. It is a remarkable fact that the lower we go in the vertebrate scale the more automatic or independent do the nerve centres of the spinal cord become; the higher we go in the scale the more they become dominated by and dependent upon nerve centres situated in the hind-brain, mid-brain and fore-brain. Hence we are prepared to find that the first tracts of nerve fibres which appear in the marginal zone are those which link together the nerve centres in the spinal cord itself. At the end of the first month the fibres of the posterior root have entered the marginal zone on the dorsal side of the cord, and have thus formed the rudiment of the posterior funiculi; these effect connections with receptive nuclei in the posterior horns. At the same time fibres which associate neighbouring or allied nuclei or centres

of the cord appear in the marginal zone of the lateral and anterior parts of the cord. These may be described as inter-segmental tracts.

Later, in the 3rd month, commences the growth of fibres within the antero-lateral marginal zone of (1) tracts which, arising from cells in the cord, are to end in hind-brain, mid-brain and fore-brain, and thus supply these higher centres with afferent impulses which are reaching the spinal centres; (2) tracts which, commencing in the hind and mid-brain, grow down to permit the higher centres to influence the lower centres in the cord. Lastly, in the 5th month, the pallio-spinal or **pyramidal tracts** commence to develop. The pyramidal tracts (crossed and direct) grow down from the cells of the motor cortex. They are not medullated until soon after birth. The pyramidal tracts are the means by which the brain controls the motor cells of the cord. In man these tracts are remarkable,

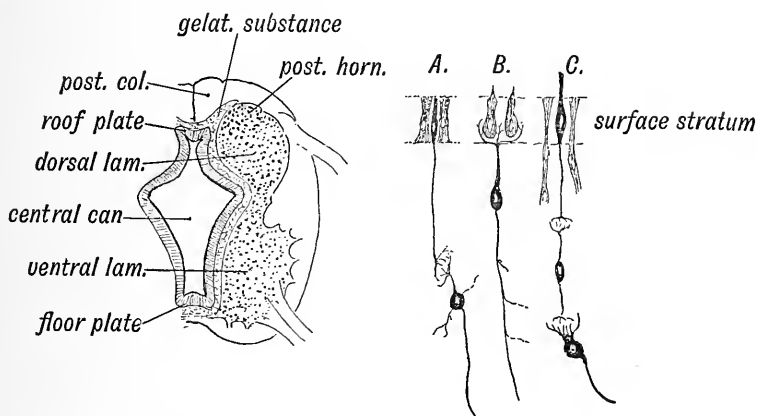


FIG. 77.—Diagrammatic Section of the developing Spinal Cord to show (1) the Roof and Floor Plates; (2) the Dorsal (alar) and Ventral (basal) Laminae; (3) the Gelatinous Tissue between the Middle and Inner Zones.

FIG. 78.—Showing Transformation of Cells of the Ectoderm to Sense Epithelium, Nerve Cells and Supporting Cells, in *A*, the Olfactory Plate, *B*, the Otocyst, *C*, the Retinal Layer of Optic Cup.

not only for their great size, but also that in addition to the crossed lateral tract, which is present in all mammals, there is also an anterior or direct tract. The anterior tract appears to be a recently evolved system; it is extremely variable in size. The only other animals which possess it are those nearest allies of man—the great anthropoid apes.

The **myelinization**¹—the formation of medullary sheaths for the fibres of nerve tracts—commences about the 4th month and is not really finished until the age of puberty is reached. The oldest tracts—the ones which are first required to carry messages—are the earliest to be medullated. The process begins in the oldest part of the fibre—the part nearest the parent nerve-cell—and spreads towards the growing tip. The great nerve tracts are ensheathed at different dates; hence it is possible to distinguish and unravel one tract from another during the period of development.

¹ Florence R. Sabin, *Amer. Journ. Anat.* 1911, vol. 11, p. 113 (Model of Tracts medullated at Birth).

Segments of the Spinal Cord.—To that part of the neural tube and neural crest which corresponds in position to a primitive body-segment, the name of **Neuromere** is given. From the cells of a neuromere are produced the posterior and anterior root of a spinal nerve on each side. The extent of each neuromere is thus marked out by the attachments of its nerve roots. At no time are the medullary plates divided into embryological segments in the same sense as the mesoderm is divided, although the neural tube probably did arise from the fusion of a series of neuromeres or ganglia, each presiding over a definite segment of the body, subsequent evolutionary changes have led to their fusion. Dr. Watt observed in a human embryo in which there were 18 body-somites, that 11 segments were to be noted in the spinal cord. These changes are related to the combination of the various segments and systems in carrying out the functions of the body. The cervical and lumbar enlargements of the cord appear in the 4th month. They contain the neuroblasts connected with the body-segments which gave rise to the upper and lower extremities. The neuroblasts are arranged, not according to the original neural segments, but rather in relationship to the movements of the limb. The group representing the hand movements lie behind (distal to) those representing movements of the forearm.

Origin of the Medullary Plates and Nerve Cells.—The medullary plates like the olfactory plates which give rise to the sense-epithelium of the nose, the otocyst from which the auditory organ is developed, and the retina are derived from the ectodermal covering of the embryo. The olfactory plate retains to the greatest extent the features of the ectoderm (Fig. 78, *A*). Its cells are of three kinds: (1) protective, (2) secretory, (3) sensory, the latter being essentially surface nerve cells in nature. A process or axis cylinder is produced from each sense cell; from its opposite extremity a sensory process is produced (Fig. 78, *A*). In worms, sense epithelial cells sink beneath the protective and secretory cells, the sensory process being drawn out to form a fibre. In the otocyst, the sensory cells produce no axis-cylinder process, but a ganglionic cell—produced from the ectoderm through the neural crest—comes into connection with it (Fig. 78, *B*). From the ganglionic cells are produced (1) a chief process or **axis cylinder**; (2) a branching process or processes—**dendrites**—from the opposite pole, which end in an arborescence round the sensory cells. To a nerve cell and all the processes developed from it the name of **Neuron** is given. In the retina, as in the olfactory plate, three types of cells are seen: (1) protective or supporting which form the fibres of Müller, (2) secretory over the ciliary processes, (3) the sensory cells, which produce an axis cylinder on one side, and a rod or cone on the other (Fig. 78, *C*). Further, by a process of division, bipolar and ganglionic cells are produced from the retinal sense cells. In the medullary plates of the spinal cord the representatives of the original ectoderm form the ependymal and neuroglial cells, the first of which may be regarded as both secretory and supporting; the neuroblasts arise by a process of division from the primary ectodermal cells. Each neuroblast gives rise to a neuron. Their axons or axis cylinders are in many cases two feet or more in length; for instance, the

motor and sensory fibres which pass from the lumbar enlargement to the muscles and skin of the foot. The nerve cells in the basal laminae are peculiar in that their axis cylinders end on muscle cells.

Malformations of the Neural Canal.¹—The fact that children are occasionally born with the medullary plates open and exposed on the head and back has already been mentioned (see Fig. 69). **Total Rachischisis**, as the condition is named, is rare; it is much more usual to find only one part of the neural tube open—either the anterior or cephalic part, giving the condition known as **Anencephaly**—absence of brain, or the posterior or lumbo-sacral part, giving the condition known as **cystic spina bifida**. The latter condition is shown in Fig. 79. As the spinal cord is followed down, it is seen to enter a cystic structure formed by a dilatation of the

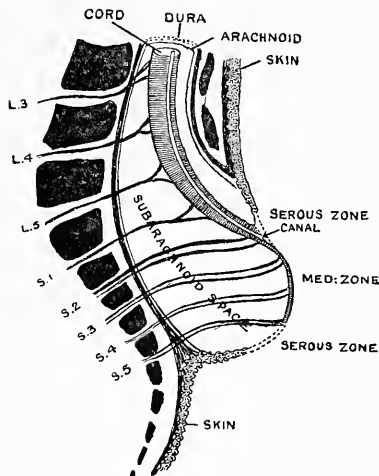


FIG. 79.—Vertical Section of the Lumbar Region to show the arrangement of parts in a typical case of cystic spina bifida.

subarachnoid space, across which the roots of the lumbo-sacral nerves pass. The projecting dome of the cyst is formed by the expanded medullary plates; hence the spinal cord appears to end on the wall of the cyst, and spinal nerves to actually arise from it. The lumbo-sacral parts of the neural tube and of the spine have never been enclosed; the cerebro-spinal fluid collects in the subarachnoid space, and the unresisting medullary plates are raised up to form part of the wall of a cystic tumour. Another form of pathological dilatation may appear after the neural tube is completely closed. In chicks hatched at abnormal temperatures fluid may collect in certain parts of the tube, thus dilating it and giving rise to cystic conditions.

Membranes and Vessels of the Cord.—When the neural tube is enclosed towards the end of the 3rd week by the upgrowth of mesoderm

¹ J. P. Good, *Journ. Anat.* 1912, vol. 46, p. 391; J. Voigt, *Anat. Hefte*, 1906, vol. 30, p. 393; W. M. Baldwin, *Anat. Record*, 1915, vol. 9, p. 365; Theodora Wheeler, *Contrib. to Embryology*, 1920, vol. 9, p. 95; E. J. Carey, *Anat. Record*, 1919, vol. 16, p. 45.

in the medullary folds, mesenchymal cells become applied to the neural tube. They form the primary sheath of the neural tube (Fig. 74, C). The sheath receives a vascular supply from each dorsal branch of the segmental arteries and veins. Branches of the vessels perforate the nerve tissue, and thus a vascular mesodermal element is added to the ectodermal neural laminae. By the middle of the second month the primary sheath has become cleft into an inner or pial layer, and an outer or arachno-dural layer. The cleft becomes the subarachnoid space, which is apparently of the nature of a lymphatic space (see p. 90).

Development of Nerves.¹—In lower fishes Kupffer found that nerve fibres were formed by the union of a chain of cells—probably ectodermal in origin, and many suppose that the nerve fibres of all vertebrates are formed in this manner, the nuclei of the chain-cells becoming the nuclei of the neurolemma. On the other hand His and Kölliker concluded that every nerve fibre is produced as a continuous outgrowth from one nerve cell, and that the cells of the sheath are mesodermal in origin. It is possible that both interpretations of the appearance presented by developing nerves are right, and that one kind of nerve fibre is produced in the first manner and another kind in the second manner. The opinion generally held at the present time is that an axis cylinder is the product of one nerve cell or neuroblast, and that the cells which surround the growing fibres and form their sheaths are derived from the neural crests, and are therefore ectodermal in origin. It is maintained by Dr. John Cameron that these surrounding cells assist in the deposition of an achromatic substance at the growing points of nerve fibres (*Journ. Anat. and Physiol.* 1906, vol. 41, p. 8). Dr. Ross Harrison found that when small parts of the medullary plates of tadpoles were transplanted or maintained alive in artificial media the outgrowth of the neurons as processes from single cells could be witnessed (*Anat. Record*, 1908, vol. 2, Nos. 9, 10).

Another theory receives support from Graham Kerr's recent investigations on *Lepidosiren*, viz. that nerve fibres are formed by the stretching of protoplasmic connections which originally exist between nerve and muscle cells.

¹ Papers on histogenesis of nerves: R. G. Harrison, *Amer. Journ. Anat.* 1906, vol. 5, p. 121; W. H. Lewis, *Amer. Journ. Anat.* 1906, vol. 6, p. 461; J. Cameron, *Journ. Anat. and Physiol.* 1907, vol. 41, p. 8; Prof. T. H. Bryce, *Quain's Anatomy*, 1908, vol. 1, p. 94.

CHAPTER VIII.

THE MID- AND HIND-BRAINS.

WHEN the neural tube is traced forwards into the head region, it is seen to undergo a marked change in form—a transformation due to a change in function. In the spinal cord the nerves arose in two rows—a dorsal sensory and a ventral motor; here the dorsal and ventral series are still represented, but a third or intermediate series has been added. This series is represented by the spinal accessory (XI), vagus (X) and glossopharyngeal (IX), facial (VII) and fifth (V) pairs of nerves. They arise from an intermediate column of cells representing in an exaggerated degree the splanchnic or visceral nerve columns of the spinal cord. Further, the central canal becomes enlarged to form the 4th ventricle. Part of the roof of the neural tube becomes reduced to a membranous lamina, forming the medullary velum and choroid plexus—a secretory mechanism. Part of the roof is specialized to form a complex mechanism (the cerebellum) for the co-ordination of the impulses dispatched to the motor cells of the spinal cord. This high degree of specialization almost obliterates the original simple nature of that part of the neural tube which forms the mid- and hind-brain. In the human embryo at the beginning of the 4th week it is seen that this part of the central nervous system retains its tubular character, while that part which is to form the hind-brain, even at this early stage, shows an imperfect segmentation into nine neuromeres. Further, the neural tube in the regions of the mid- and hind-brain, as in the spinal cord, lies over the notochord (Fig. 80). The notochord ceases at the junction of the mid- and fore-brain. The developing walls of the mid- and hind-brain show the same three zones as were seen in the spinal cord—inner or ependymal, middle or mantle and outer or marginal. We shall find, too, the same division of each lateral neural plate into basal and alar laminae.

A reference to the relationships of the hind-brain, during the 4th week of development (Fig. 80), serves to explain why the vital centres of the body—those which are concerned in the regulation of respiration, circulation, deglutition and digestion, come to be placed in its walls. At this time the hind-brain lies over the pharynx, with its aortic arches, and its gill-pockets—representing the breathing mechanism of fishes. When lungs arise the control of respiration still lies in the original respiratory centres of the hind-brain. The heart, too, lies directly under, or ventral to, the hind-brain (Fig. 80); hence the centres for circulation are placed there.

The fore-gut, from which the mouth, pharynx, oesophagus, trachea, lungs, stomach and liver are to arise is also placed in the territory of the hind-brain. Its relationship to the otocyst, however, is to prove the most important. From that structure is to arise a vestibular or balancing mechanism designed to supply information concerning the position and movements of the head. The cerebellum and pons which so transform the simple tubular hind-brain, arise in connection with the vestibular nuclei. One other point may be noted before proceeding to follow the transformation of the hind-brain into medulla oblongata, cerebellum and pons. The mid-brain is interpolated between the spinal cord on the one side and the mid- and fore-brain on the other ; hence it becomes the great

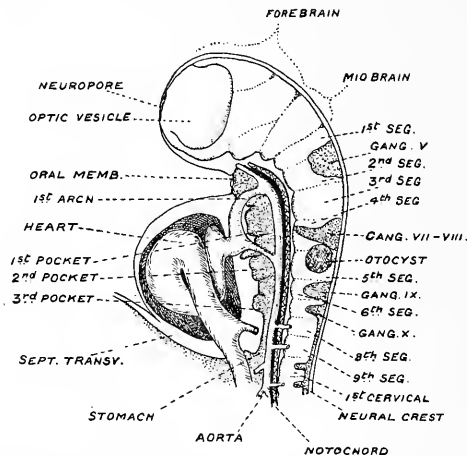


FIG. 80.—Showing the tubular form, the neuromeres and relations of the Mid- and Hind-Brain in a Human Embryo in which there were 18 body somites—in the 4th week of development. (Crawford Watt.)

highway for the nerve tracts which are developed to link brain and spinal cord into a functional whole. Throughout the greater part of the second month the hind-brain forms a little less than half of the total neural tube.

The Fourth Ventricle.—The cavity or neural canal of the hind-brain becomes the fourth ventricle. In its floor are developed, out of the **basal** or **ventral** and **alar** or dorsal **laminae** (Fig. 81) of the neural plates, the pons and medulla. In its roof are developed the cerebellum, the superior and inferior medullary vela.

Basal and Alar Laminae of the Medulla.—The basal and alar laminae of the neural tube become flattened out to form the floor of the hind-brain. At the end of the 4th week each medullary plate shows three zones : an inner or ependymal where new cells are being produced ; a middle or mantle zone in which neuroblasts, neuroglial fibres and young nerve fibres are being differentiated and an outer or marginal zone. By the 6th week the disposition of the nuclei connected with the cranial nerves in the mantle zone can be made out. The grouping of the nuclei

as seen in a diagrammatic section across the hind-brain is shown in Fig. 82. In the mantle zone of the basal lamina are three columns of motor cells—the columns being much interrupted as they are traced from the lower to the upper end of the hind-brain. These are: (1) the **somatic motor**, continuing upwards the somatic cells of the anterior horn and

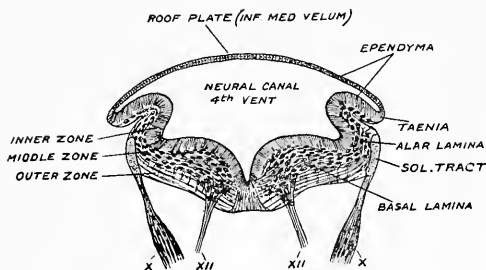


FIG. 81.—Section across the Hind-Brain of a Human Embryo in the 6th week.

supplying muscles derived from the body somites; from this column arise the XII and VI nerves. (2) The **lateral somatic motor**, supplying striped muscle which was first evolved for the movement of gill-arches; from this column arise motor fibres of XI, X, IX, VII and V. The nucleus ambiguus forms part of the column. (3) The **splanchnic motor** nuclei, giving origin to fibres distributed to the musculature of the heart,

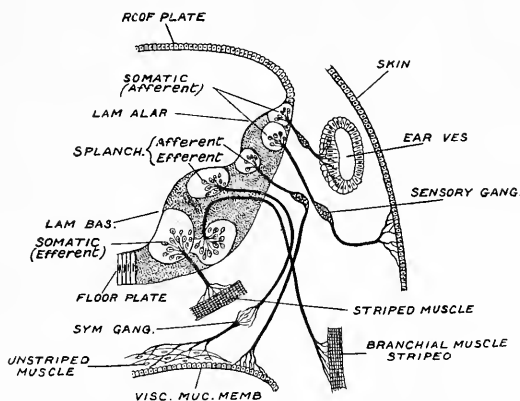


FIG. 82.—Diagrammatic section across the Hind-Brain to show the grouping of cranial nerves and their nuclei. (After Elliot Smith.)

lungs and alimentary canal—represented by the dorsal nuclei of IX and X. In the alar lamina are differentiated two main groups or columns of sensory or reception nuclei: (1) **splanchnic**, which receive the ingrowing fibres of the IX-X nerves—and therefore are in connection with the pharynx, heart, lungs and alimentary canal, receiving afferent impulses from all including those of taste; (2) **somatic**, corresponding to the posterior horn cells of the spinal cord and receiving fibres in series with the posterior roots of spinal nerves. The posterior root fibres in the cranial series are

represented by the sensory root of the Vth and by the VIIIth nerve—both vestibular and cochlear divisions. The VIIIth nerve and its ganglia were probably derived from the same system as gave rise to the complex sensory organs of the lateral line of fishes, and should be distinguished from the ordinary somatic group. We have seen how the posterior funiculi are formed in the marginal zone of the spinal cord by fibres of the posterior roots. The sensory fibres of the cranial nerves also form tracts in the marginal zone; the solitary tract is formed by fibres of the IXth and also of the Xth and VIIth. The vestibular and fifth nerves also form tracts—the latter being particularly extensive. At first these tracts lie near the surface of the hind-brain, but in the sixth week they become overwhelmed and buried by vast migrations of neuroblasts.

Neurobiotaxis. In Fig. 83, *B* is given a diagrammatic section across the right half of the neural plate of the hind-brain at the sixth week of develop-

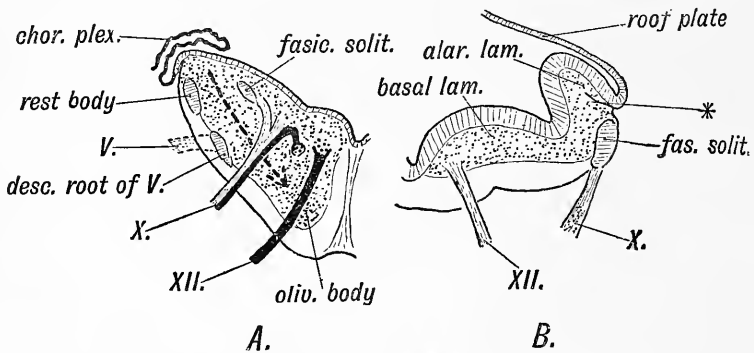


FIG. 83, *A*.—Diagrammatic Section of a Foetal Medulla to show the relative positions of the Nuclei connected with the Somatic and Splanchnic Nerves, and the Origin of the Olivary Body. The Motor Nerves, both Somatic and Splanchnic, are represented black. The arrow indicates the route of migration of the Cells of the Olivary Body.

FIG. 83, *B*.—The Alar and Basal Laminae of the Hind-Brain at the beginning of the 6th week to show the superficial position of the sensory root of the Vagus. (Compare with *A*.) The rhombic lip and the point at which the root of the 5th Nerve and Restiform Body will be formed is indicated by an asterisk. (After His.)

ment, showing the solitary tract in the marginal zone of the ventral surface; in Fig. 83, *A* is given the condition in the 8th week, showing the fasciculus solitarius buried deeply—much nearer the dorsal than the ventral aspect of the medulla. What has happened is this: swarms of neuroblasts have been produced in the ependymal zone near the dorsal margin of the alar lamina—at the rhombic lip marked by an asterisk in Fig. 83, *B*. In the spinal cord the posterior horn is the latest site of neuroblastic production; in the hind-brain this tendency to new production of neuroblasts in the dorsal margin of the alar lamina has become enormously heightened. The arrow in Fig. 83, *A* shows the direction of the swarm; they invade the marginal zone, burying the solitary tract, and group themselves as they approach the floor plate in the middle line, to form the inferior olivary body; the superior olivary body and the great terminal or receptive nuclei—the gracile and cuneate nuclei—are formed in the same way.

Dr. Ariens Kappers¹ in his studies on the medulla in 1907 was struck by the apparent evolutionary and developmental movement of the nuclei of motor nerves; they were drawn towards the terminal nuclei from which they received their chief incoming stimuli or messages.

For example he noted a forward movement of the motor nucleus of the XIIth towards the receptive nuclei of the IXth and Xth; of the VIIth towards the descending root of the Vth, while the nuclei of the XIth for the sternomastoid and trapezius tend to spread backwards in the spinal cord towards the receptive nuclei of the neck and shoulder. To the law or force which regulates the mass-movement or migration of neuroblasts Kappers gave the name—**Neurobiotaxis**. We have just mentioned the migrations which give rise to the olivary nuclei of the medulla, but we shall find, as we ascend the brain stem—to cerebellum and pons, to mid-brain and basal ganglia and particularly to the cerebrum itself—that neuroblastic migration is the basal principle of development and transforms the simple embryonic neural tube into the complexities of the adult brain. In the spinal cord neuroblasts are confined to the mantle zone, but in the hind-, mid- and fore-brains they invade the marginal zone and there establish their chief centres. The cortex of the cerebellum and cerebrum are produced by a neuroblastic invasion of the marginal zone. Nor are the mass-migration of nerve-cells really different from other manifestations of living cells. Outgrowing processes from the neuroblasts of the spinal ganglia and spinal cord spread into the limb buds and reach their destinations unerringly—drawn and regulated by some obscure force; Dr. Ross Harrison found that if a limb-bud was transplanted, the strange nerve fibres which entered it were attracted and moulded to a normal supply by some influence in the tissues of the bud. The force which attracts the wandering defensive cells of the body to a site of infection is probably of the same nature as that which regulates the migration of neuroblasts.

Inferior Medullary Velum.—When a section is made across the hind-brain of an embryo in the 6th week of development, the same parts are seen as in the spinal cord except that the roof plate has become enormously expanded to form the inferior medullary velum. The extent, shape and attachments of the roof plate are shown in Fig. 84; it is diamond shaped, its hind angle being continuous with the roof plate of the spinal cord, its front angle with the roof plate of the mid-brain, while its lateral angles mark the sites of the two lateral recesses of the 4th ventricle. Its upper lateral margin is attached to the border of that part of the alar lamina in which the cerebellum is to arise; its lower lateral margin is attached to the **rhombic lip**, the dorsal border of the medullary part of the alar lamina. This border is folded outwards (Fig. 81). The shape of the roof plate, or inferior medullary velum, is altered by remarkable changes which set in during the 6th week (Fig. 84); growth changes cause the hind-brain to be folded, producing the pontine bend and bringing the cerebellar part of the hind-brain against the medullary. The inferior medullary velum becomes

¹ See his more recent statement, *Journ. of Nerv. and Mental Diseases*, 1919, vol. 50, p. 1. Also Dr. Davidson Black, *Journ. Comp. Neur.* 1917, vol. 27, p. 467; vol. 28, p. 379.

drawn out transversely. It is at this time that choroidal villi are produced on its ventricular surface, first in a transverse row extending from lateral recess to lateral recess and subsequently over its entire surface. At the same time secretion of cerebro-spinal fluid commences¹; the fluid percolates through the velum at three places—middle of the roof and at the lateral angles. At a later date (3rd month) the foramen of Magendie and the openings of the lateral recess appear at the points of percolation. The subarachnoid spaces begin to form at the sites of escape and from there extend.

As shown in Fig. 88, the velum is continuous with the cerebellum above and the roof of the central canal of the cord below. In the posterior margin of the cerebellar plates are developed: (1) the nodule, (2) the flocculus,

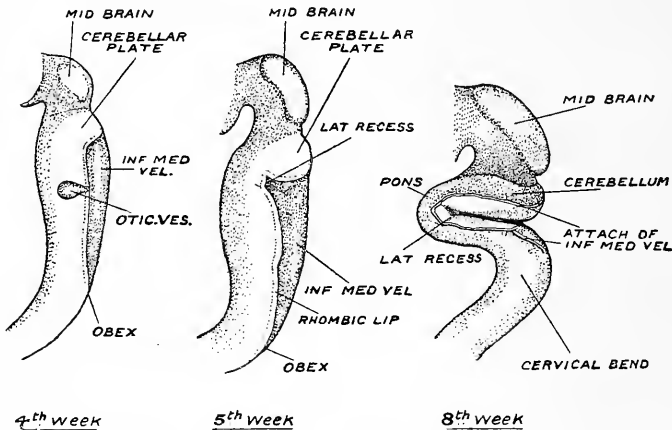


FIG. 84.—Showing the origin of the Inferior Medullary Velum from the roof plate of the Hind-Brain.

(3) the peduncle of the flocculus between 1 and 2 (Figs. 89, 90). Hence the inferior medullary velum ends above in these structures. The obex and ligula, thickenings or ridges found on the margins of the 4th ventricle, mark the attachment of the roof plate or velum to the rhombic lip of the medullary plates. They represent the attached margin of the velum. The velum is also attached to the restiform body which is developed in the upper margin of the alar lamina. Over the opening of the central canal of the spinal cord into the 4th ventricle there is often a fold formed by the union of the alar laminae (see J. T. Wilson, *Journ. Anat. and Physiol.* 1906, vol. 40, p. 210).

The velum is to be regarded as a part of the neural tube, specially modified for the purpose of secreting the cerebro-spinal fluid which fills the central canal and subarachnoid systems. This fluid may help to support the central nervous mass in a mechanical sense, but its rapid secretion, its circulation and chemical composition point to some more important

¹ I have followed the account given by Dr. Lewis H. Weed for the developing pig. See *Anat. Rec.* 1916, vol. 10, p. 256.

nutritive or regulatory influence on the neural centres. The ectodermal cells retain the primitive columnar type, and form an epithelial covering over inflexions and processes of the pia mater which is derived from the mesodermal covering of the neural tube.

Cerebellum.¹—At the beginning of the 2nd month the cerebellum is still represented by simple right and left alar plates (Figs. 85 and 93)

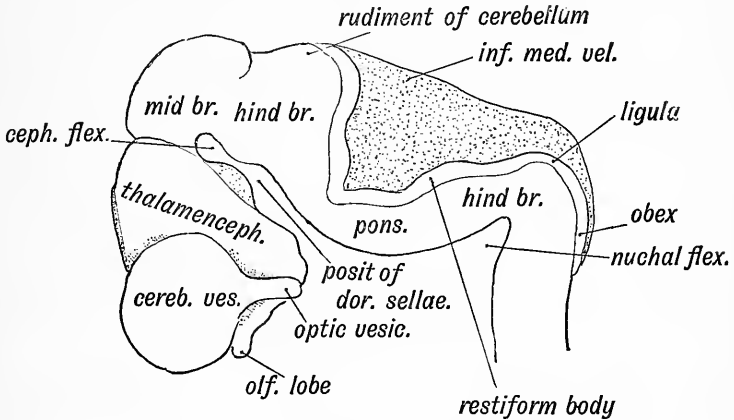


FIG. 85.—Lateral View of the Cephalic Part of the Neural Tube in a 5th week Human Embryo. (After His.)

which show the usual triple stratification—an internal proliferating ependymal zone, a middle neuroblastic and an outer marginal meshwork. In the frog a plate-like cerebellum is retained (Fig. 86), for the amphibia have but an imperfect power for sustained co-ordination of their limbs

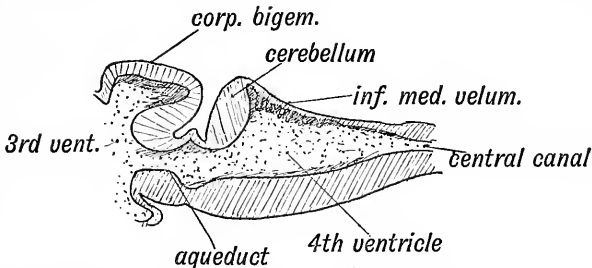


FIG. 86.—Median Section of the Cerebellum and 4th Ventricle of a Frog.

during locomotion on land. By the end of the 2nd month (Fig. 87) there has been an active proliferation of neuroblasts in the cerebellar plates; they fuse in the middle line to form the vermis or median lobe, and now bulge into the 4th ventricle, much as they do in the frog. What has happened may be best gathered from Fig. 87. The reception nucleus for the VIIIth nerve is developed in the rhombic lip near the lateral recess;

¹ I have followed the accounts given of the cerebellum by Elliot Smith (See Cunningham's *Text-Book of Anatomy*, 1913); and by Streeter (see Keibel and Mall's *Manual of Human Embryology*, 1912). See also Dr. Sven Ingvar, *Folia Neurobiologica*, 1918.

through the vestibular fibres of the VIIIth nerve this nucleus will receive impulses which make it the chief recipient of messages needed for the co-ordination of muscles. Elliot Smith regards the cerebellum as a product of the vestibular nucleus. Hence the proliferation of neuroblasts at the rhombic lip and their spread into the cerebellar plates. In the 3rd month neuroblasts invade the marginal zone of the plates and lay the basis of the molecular layer of the cortex. The cells of Purkinje—although not fully differentiated until after birth—take up their stations at the junction of the mantle and marginal zones.

At the time the cerebellar plates are being thus invaded in the 3rd month, in this way a cellular basis for the cortex being laid down, other cells, arising in the rhombic lip, invade the adjacent basal laminae—the parts which will become the pons (Fig. 87). There they lie in the path of fibres descending from the frontal cortex and thus bring the cerebellum

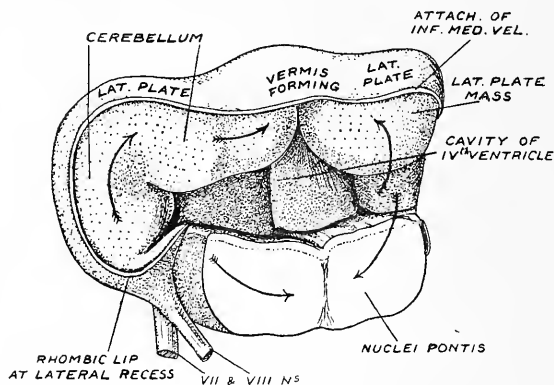


FIG. 87.—The Human Cerebellum at the end of the 2nd month of development. (After Streeter.) The arrows show the direction of the migration of the Pontine and Cerebellar Nuclei.

into touch with the cerebrum. The restiform body begins to form in the second month, and by this means the cerebellum is placed in connection with the recipient nuclei of the cord and medulla. The dentate and other central cerebellar nuclei are isolated, the dentate nuclei being linked with the red nuclei of the mid-brain by the superior peduncles. In the differentiation of the cerebellum are to be seen numerous illustrations of the law of neurobiotaxis enunciated by Kappers.

Differentiation of Lobes.—At the end of the 3rd month (Fig. 88) the cerebellum has assumed a dumb-bell form—the lateral elevations representing the right and left lobes which are united by a median plate—the vermis. The cortex has already commenced to expand, as may be seen by the early appearance of transverse fissures on the vermis. It is at this period that the cerebellar plate becomes demarcated into **anterior, middle and posterior primary lobes**, these being separated by two transverse grooves or fissures—the first and second fissures (Elliot Smith). Since these three primary divisions are to be recognized in nearly all mammalian cerebelli, they must be of fundamental importance. Quickly succeeding these two primary

fissures there appear two others, one which divides the median part of the posterior lobe—the post-nodular fissure—and the other the anterior lobe (Figs. 89, 90). The post-nodular fissure may appear in the human brain before the *fissura secunda*. Thus, at the end of the fourth month four fissures are seen to be developed in the human cerebellum (Fig. 89). The

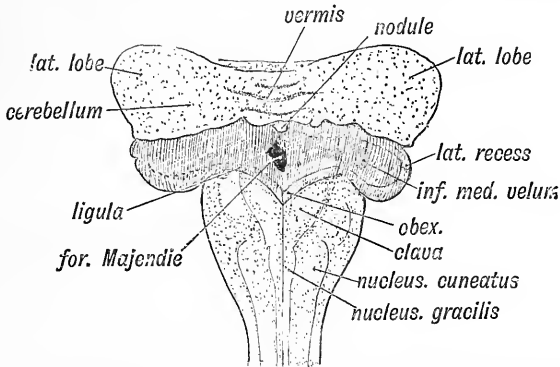


FIG. 88.—Diagram of the Cerebellum and of the Attachments of the Inferior Medullary Velum at the end of the 3rd month of development. (After Kollmann.)

rapid growth of the cerebellum, with the pressure of the cerebrum above or in front, and the resistance of the occipital bone below or behind cause the plate-like form to be replaced by one which is wedge-shaped in section, with an upper and lower surface. The minor sulci and fissures of the cerebellum appear between the 5th and 7th months of foetal life.

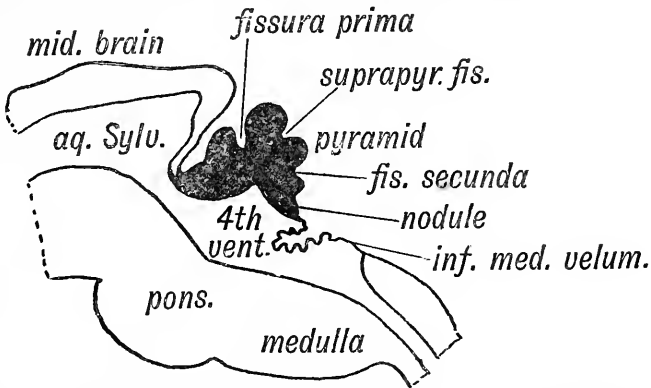


FIG. 89.—Diagrammatic Section of the Cerebellum of a Human Foetus early in the 4th month, showing the folding of the Cerebellar Plate. (After Kuitian and Elliot Smith.)

Parts derived from the Posterior Primary Lobe (Figs. 89, 90, A, B).—From the median part arise the nodule and uvula separated by the post-nodular fissure. From the lateral parts arise the flocculus and para-flocculus, which represent the oldest of all the distinctive parts of the cerebellum, and the first to become differentiated in the human organ. The

para-flocculus, part of which fills the subarcuate fossa in the temporal bone (p. 236), becomes reduced to a vestige in man and the anthropoids (Fig. 90, *A*).

Parts derived from the Anterior and Middle Primary Lobes (Figs. 89, 90, *A*, *B*).—From the anterior primary lobe arise the lingula, central lobe, and alae, the culmen and the anterior crescentic lobes. The rest of the cerebellum, comprising by far its greater part, arises from the middle lobe. It represents an addition to the older and more primitive parts represented by the anterior and posterior lobes, and hence has been named the **neocerebellum**. The median part forms the pyramid and the clivus, separated by a deep fissure. The lateral parts undergo an enormous development in higher primates. In man the tonsillar and biventral

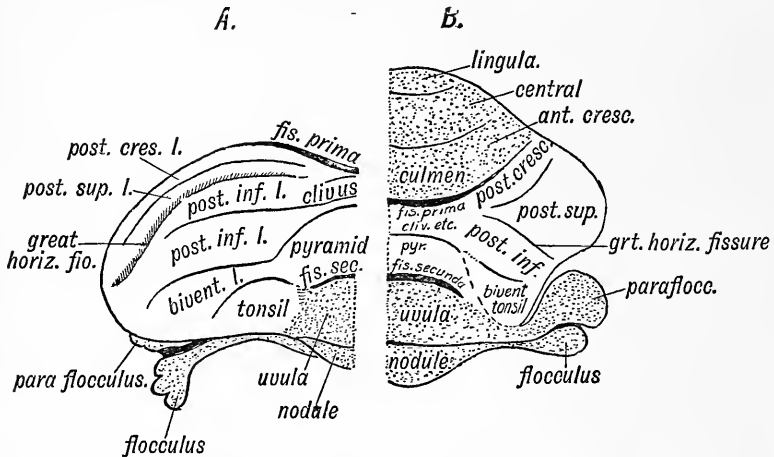


FIG. 90, *A*.—Left half of the Cerebellum of a Foetus of 5 months, seen on its inferior aspect. Only the middle and posterior primary lobes are exposed. The parts forming the posterior lobe are stippled. (After Elliot Smith.)

B.—Right half of a typical Mammalian Cerebellum, spread out so as to show the anterior, middle and posterior lobes. The anterior and posterior lobes are stippled. The fissures and parts are indicated by the terms used in human anatomy in order that the peculiar features of the human cerebellum may be made evident. (After Elliot Smith.)

lobes attain a very great size. The great development of the lateral parts of the middle primary lobe during the 5th and 6th months, leads to the formation of the great horizontal fissure (see Figs. 90, *A* and *B*).

The **Superior Medullary Velum** is part of the roof plate of the 4th ventricle which remains between the superior peduncles. The vestigial laminae which cover it form the lingula (Fig. 89).

Three points in connection with the development and comparative anatomy of the cerebellum are especially worthy of attention :

(1) It arises from the alar laminae, which are directly connected with afferent or sensory nerves only ; further, the nuclei in the mesencephalon, pons and medulla, with which it is connected, arise from the alar laminae.

(2) The part of the neural tube from which the cerebellum arises is the vestibular neuromere—the one to which the internal ear becomes closely linked.

(3) The cerebellum reaches its greatest development in primates amongst mammals; it is also greatly developed in swimming vertebrates. In primates, as in swimming mammals, the equilibrium of the body is finely adjusted. On embryological grounds alone we would infer that the cerebellum is part of a sensory mechanism. Clinical and experimental observations indicate that its main function is to co-ordinate the various muscles of the body in performing definite acts. It is therefore on the afferent nerve system arising from the muscles, joints and bones, that the cerebellum has been developed, but its position was determined by the nuclei of the vestibular nerves, cells of which invade the embryonic cerebellar plate.

MID-BRAIN OR MESENCEPHALON.

By the end of the 3rd month the mid-brain is becoming overshadowed by the preponderating growth of the fore- and hind-brains, and by the 6th month is reduced to the peduncular body which unites cerebrum with cerebellum, its ventricle or canal becoming reduced to the aqueduct which unites the 4th ventricle to the 3rd. With the mid-brain we reach the anterior limit of the primitive neural tube; it lies over the terminal cephalic part of the notochord (Fig. 80); two cranial nerves (III and IV), corresponding to the anterior roots of spinal nerves, arise from it. A section across the mid-brain in the 4th week of development, reveals the same divisions as in the cord—lateral neural plates made up of basal and alar laminae, united by a roof plate and a floor plate. The same three zones arise—ependymal, mantle and marginal. In the 3rd month the quadrigeminal plate develops on the dorsal part of its alar laminae, much in the same way as the cerebellum arises within the alar laminae of the hind-brain. The neuroblasts invade the dorsal marginal zone, and evolve into a formation which may be described as a cortex. The quadrigeminal plate which thus arises on the dorsum of the mid-brain may be regarded as primary receptive centres for the nerve of sight (the optic tracts), and in birds this formation assumes great size and importance. The necessity of linking the receptive nuclei for sight with those for hearing is apparent; hence we find the cochlear nuclei connected with the quadrigeminal formation by the lateral lemniscus. In the development of the mid-brain we see the quadrigeminal plate become divided into the *inferior colliculus*—in which the cochlear tract ends—and the *superior colliculus*, which receives fibres from the retina. Thus, in the main the mid-brain is connected with sight; in the basal laminae arise the nuclei for the IIIrd and IVth nerves—the chief source of motor supply for the muscles of the eye-ball (Fig. 93). From the mid-brain arise also sensory fibres of the Vth nerve which go to the orbit. They differ from all other sensory fibres in having their cell bodies implanted in the wall of the neural tube. From the 3rd month of development onwards the mid-brain becomes the highway of developing efferent nerve paths which unite the basal masses and cortex of the fore-brain with the nuclei in the pons, medulla and spinal cord, and of afferent or sensory paths which connect the nuclei of the cord, medulla and cerebellum with the basal masses of the fore-brain. The cerebral

cortical paths develop in the marginal zone of the basal plates and form the crura cerebri, while the afferent paths—the median lemniscus—develops in the mantle zone—the tegmentum. In this zone, too, appears the red nucleus, but as yet its neuroblasts have not been traced to their source.

The Three Neural Flexures (see Figs. 80, 84, 85).—The **pontine flexure**, a convexity forwards of the pons, has already been mentioned; it is the result of the elongation of the neural plates of the hind-brain due to the proliferation of the neuroblasts and the production of the cerebellar plates. The **nuchal flexure** is concave forwards, and occurs between the medulla and cord. The latter is compensatory and of but small import; on the other hand, the **anterior flexure**, whereby, in the third week of

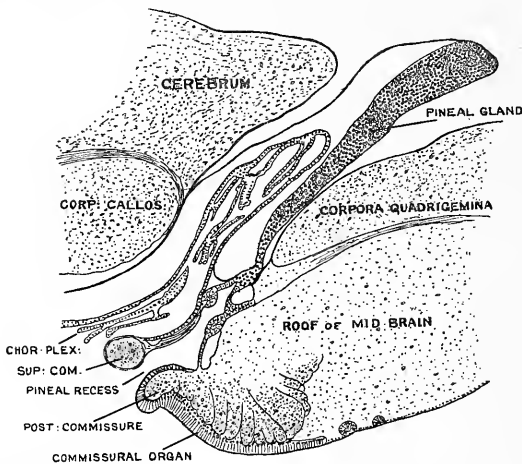


FIG. 91.—Section of the anterior part of the Roof of the Mid-Brain of a Cat, to show the subcommissural organ. (Dendy and Nicholls.)

foetal life, the fore-brain appears as a downward and forward development until it comes to lie on the ventral aspect of the cephalic end of the notochord, leads to a great alteration in the form and relationships of the fore- and mid-brains, and is of great importance (Fig. 85). Even in the embryos of the lowest vertebrate types the expansion and bending of the anterior end of the neural tube is apparent. The mid-brain, by this flexure, comes to be, for a short time, the most anterior part of the neural canal; the fore-brain is doubled back under the notochord. Round the projecting end of the notochord—projecting between the mid- and fore-brains—are developed the posterior clinoid processes and dorsum sellae. The dorsum sellae marks the position of the anterior flexure in the adult brain. The tentorium cerebelli is developed between the mid-brain and fore-brain, and lies at first at right angles to the axis of the mid-brain, but the subsequent great growth of the cerebrum forces it backwards and downwards until it becomes a horizontal partition between the cerebellar and cerebral chambers of the skull.

Subcommissural Organ.—For some time it has been known that the ependyma on the roof of the mid-brain of lower vertebrates, immediately behind the posterior commissure (see Fig. 91), is modified to form a peculiar area of high columnar cells. The cells are related to a certain very large fibre (Reissner's fibre), which descends ventral to the central canal of the spinal cord in fishes and amphibians. Recently Dendy and Nicholls have shown that this ependymal structure, to which they have given the name of subcommissural organ, occurs in all vertebrates, including man. It is quite apparent in the human foetal brain, but is soon reduced to a vestige. The fibres are not nervous in nature. The function and significance of the structure are unknown.¹

Constitution of the Mid- and Hind-Brain.—We have traced the development of the neural tube in a forward direction, and have reached

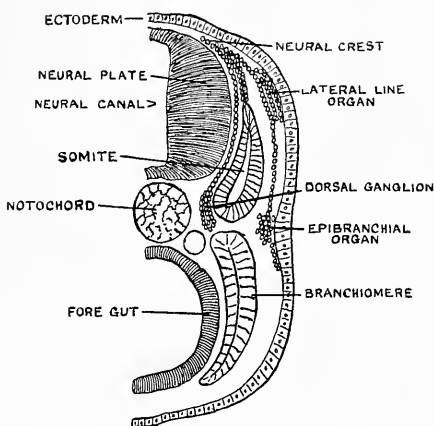


FIG. 92.—Diagrammatic Section across the posterior region of the Head of Ammoeetes—the immature form of the Lamprey—to show a Branchiomere and the ganglia derived from the Neural Crest of the Hind-Brain. (After Froriep.)

the point where the mid-brain passes into the fore-brain. On the roof the point of transition is marked by the posterior commissure (Fig. 91); below the floor the notochord ends (Fig. 80). We have reached the end of the neural tube proper; the part in front—the fore-brain—appears to have arisen in connection with two great organs of sense—the nose and eye. We find that the neural tube, when it enters the region of the head, becomes greatly altered in its constitution. This is due, not only to the development of special parts such as the pons, the cerebellum, quadrigeminal plate and special nerve tracts which unite the cerebral and spinal centres, but especially to the fact that the structure of the head is older and more complex than that of the body. In the head region another element appears—a **ventral** mesodermic somite or branchiomere—in addition to the **dorsal** mesodermic somite seen in the trunk region (Fig. 92). The branchiomeres give rise to the gill arches, which are so apparent in the human embryo at the end of the first month. In the mid- and hind-brain special centres and

¹ See Nicholls, *Quart. Journ. Mic. Sc.* 1912, vol. 58, p. 1.

nerves are developed in connection with the gill arches. In the spinal cord there were two columns of motor nerves in the basal lamina, one for the somatic or voluntary muscles of the body, another for the visceral musculature—the splanchnic—but here a third or intermediate column is added—the motor cells for the muscles connected with the gills (Fig. 82). The branchial—or lateral somatic nerves are represented in the mid- and hind-brain by the motor or ventral root of the Vth nerve, by the motor part of the VIIth, by the parts of the IXth, Xth, XIth, which supply striated muscles. The presence of branchial arches in the head region gives rise to a more complex arrangement of the nerve ganglia (Fig. 93). In the trunk region the neural crest gave origin to posterior root ganglia, the ganglia of the sympathetic chain (prevertebral), and other ganglia stationed in front of the spine. In the regions of the mid- and hind-brain the neural crest also is developed, but besides giving rise to ganglia (see Figs. 92, 93) representing the posterior root ganglion and sympathetic ganglia found in the region of the trunk, it also gives origin to a lateral mass of nerve cells, from which the sensory fibres to the gills are produced. Associated with this lateral mass are also cellular formations representing two rows of sense organs¹—an upper, the organs of the lateral line; a lower, the epibranchial sense organs. In man only vestiges of these sense organs appear. The ultimate fate of the epibranchial rudiments is not known for certain, but it is probable that some of their cells are included in the ganglia at the trunks of the VIIth, IXth and Xth nerves.

Segmental Arrangement of Cranial Nerves.—We have seen that nine neuromeres can be recognized in the hind-brain at the 4th week of development (Fig. 80), and we may assign a double segmental origin to the mid-brain. But when we look at the ganglia and nerves of an embryo in the 6th week of development (Fig. 93) it will be realized that it is impossible to assign a cranial or head segment to each of these. In the human embryo it is easy to see that the VIIth nerve enters the second or hyoid arch and may be regarded as the nerve of the hyoid segment—which may be reckoned the 3rd segment of the head, but the nerve of the segment arises from the 4th neuromere of the hind-brain, while the nucleus of the VIth apparently arises from the Vth. Meanwhile we regard both of these neuromeres as belonging to the third cranial segment. In this segment of the head, then, we have an approach to the full complement of nerve elements found in a typical cranial segment. The somatic motor fibres are represented by the VIth nerve (to the external rectus); the lateral somatic motor or branchial, by the motor fibres of the VIIth or facial; the splanchnic efferent or motor by the secretory fibres of the chorda-tympani of the VIIth; the afferent or splanchnic sensory by the gustatory fibres of the VIIth (chorda tympani and great superficial petrosal); the somatic sensory fibres by the VIIIth or auditory nerve. The cochlear and vestibular ganglia represent a posterior root ganglion; the submaxillary ganglion—a vagrant sympathetic ganglion. Thus the 4th neural segment has become associated with the hyoid (2nd visceral) arch, the eye and the ear.

¹ The formation here named lateral line "organ" is better termed the dorsolateral placode, and the epibranchial "organ" epibranchial placode.

In the other segments there have been great changes and reductions. As regards the nerves of the first *cranial* segment, only its somatic motor nerve—the IIIrd nerve—remains; its posterior root and ganglion are represented by the ophthalmic division of the Vth nerve. The ciliary ganglion represents the sympathetic ganglion of this segment; the fibres from the IIIrd to this ganglion, the efferent or motor splanchnic fibres. In the ciliary ganglion there may also be motor splanchnic cells, carried out on the fibres of the IIIrd nerve. The nerves of the second segment are represented by the IVth or trochlear nerve (somatic motor), the nerves to the muscles of mastication (lateral somatic or branchial root), the somatic sensory by the maxillary and mandibular divisions of the Vth nerve. The sensory root of the Vth nerve has spread its dominion until it now forms

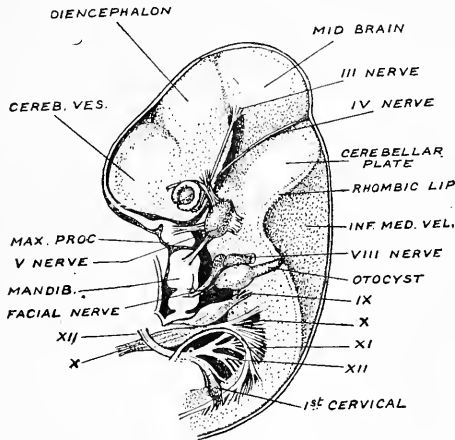


FIG. 93.—The Nerves and Ganglia of the Mid- and Hind-Brain of an Embryo at the end of the 6th week of development. (After Streeter.)

connections with all the segments of the mid- and hind-brains, and even reaches the upper part of the spinal cord. There are no sensory somatic fibres in the nerves of the 4th, 5th, 6th and 7th cranial segments with the exception of the auricular branch of the vagus. The IXth or glosso-pharyngeal is the nerve of the 4th cranial segment and contains lateral somatic, efferent and afferent splanchnic fibres. The vagus and bulbar roots of the spinal accessory represent the splanchnic efferent and afferent nerves of the 5th, 6th and 7th segments—the most important segments in the neural tube, for they contain the nerve centres which dominate the heart, the lungs and the greater part of the alimentary canal. The somatic motor roots of the 5th, 6th and 7th cranial segments are represented by the fasciculi of origin of the XIIth nerve—the motor nerve of the tongue; they arise from the 8th and 9th neuromeres. It will be thus seen that embryology and comparative anatomy supply a clue to the manner in which the cranial nerves are arranged. The basis of that arrangement is strictly a physiological one, but the specialization in certain segments, which has occurred in the course of evolution, has destroyed the original simplicity

of their arrangement.¹ Further mention of the cranial nerves will be made in dealing with the nose, eye, ear, face and visceral arches.

In the human embryo vestiges of posterior roots and ganglia may appear with the hinder hypoglossal fasciculi (Froriep's ganglion); we may infer that at one time the occipital segments had nerves with anterior and posterior somatic roots. Streeter also observed that the spinal rootlets of the XIth nerve have vestigial ganglia (visceral sensory) on them when first formed (Fig. 92).

¹ For segmentation of hind-brain see F. P. Johnson, *Anat. Record*, 1915, vol. 10, p. 209; J. C. Watt, *Contrib. to Embryology*, 1915, vol. 2, p. 1; H. L. Barniville reference, p. 47; Prof. D. Waterston, *Journ. Anat.* 1915, vol. 49, p. 90.

CHAPTER IX.

THE FORE-BRAIN OR PROSENCEPHALON.

The Origin of the Cerebrum.—It is in connection with the fore-brain that the most distinctive and most complex of all human structures arises—the cerebrum. If we confine our attention purely to the developmental changes which occur in the fore-brain of the human embryo, we shall understand very imperfectly the origin and nature of the human brain. It is true that on developmental evidence alone we may infer that the

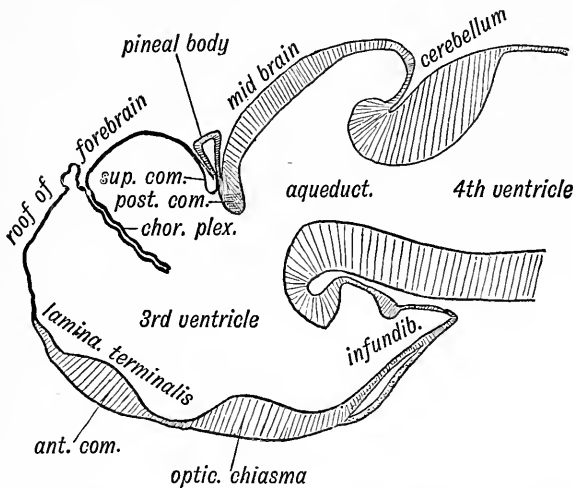


FIG. 94.—Longitudinal Section of the Brain of a Larval Fish, to show the primary form and relations of the fore-brain. (Kupffer.) Note especially that the whole roof is formed by a choroidal velum.

fore-brain, although situated at the anterior extremity of the neural tube, does not represent a prolongation of all the elements of the tube, but only of its alar or dorsal laminae, which we know to be sensory in their nature. We may infer that the fore-brain belongs to the sensory part of the nervous system—not to its motor or basal lamina. To obtain a proper appreciation of the fore-brain, however, one must study this structure in the lowest of vertebrates—the Lamprey. In Fig. 95 the brain of this primitive fish is represented. The fore-brain is made up of two parts—a posterior—the **thalamencephalon** or **diencephalon**, with which the retinae and optic tracts are connected, and an anterior or **telencephalon**, in which

the olfactory nerves terminate. The two parts of the fore-brain have thus arisen in connection with the sense of sight and the sense of smell; secondary nerve masses have arisen in these two parts of the fore-brain—the optic thalamus in the posterior, and the corpus striatum in the anterior; but the optic thalamus receives not only nerve tracts connected with the sense of sight, but other sensory tracts connecting it with all the systems of the body—skin, muscles, joints, ear, etc., and thus becomes a higher centre for the control of lower centres. The corpus striatum—the secondary mass in the anterior or olfactory part—the telencephalon—also receives tracts from the gustatory, and other lower centres besides those from the olfactory tracts. In the brain of the lamprey the mid-brain and the two parts of the fore-brain form a “federation of centres.”¹ In mammals the telencephalon becomes the dominant part; the cerebral hemispheres arise from it. Thus our cerebral hemispheres have arisen in connection

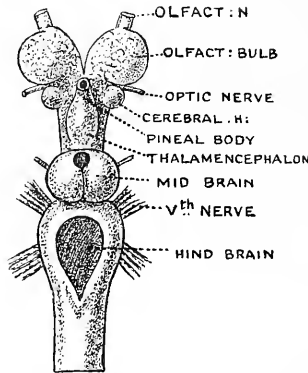


FIG. 95.—The Brain of the Lamprey from above. (After R. H. Burne.)

with parts which have become insignificant—the olfactory nerve centres. The telencephalon has received and formed communications with all parts of the central nervous system, and become the central exchange of all sensory impulses and also the seat of consciousness.

The Fore-Brain of the Human Embryo.—In the 4th week of development there is a resemblance between the human fore-brain and that of a fish; both are of a simple vesicular form (compare Figs. 94 and 96). In some respects the fish's brain is the more instructive, because its parts are clearly differentiated. In the fish the roof of the 3rd ventricle—the name given to the central canal of the thalamencephalon—contains no nerve tissue; it is membranous, and forms a choroid plexus. The pineal body arises from the posterior part of the roof, immediately in front of the posterior commissure (Fig. 94). The representatives of those parts are seen in the roof of the 3rd ventricle of the human embryo (see Figs. 96, 97, 98). On the narrow floor of the 3rd ventricle are seen the infundibular part of the pituitary body and the optic chiasma—or the plate in which

¹ The phrase is Professor Elliot Smith's, whose researches on the evolution of the brain form the basis of the account given here.

the chiasma will be formed. In both the fish and the human embryo the anterior wall of the 3rd ventricle is formed by a plate of neural tissue—the **lamina terminalis**.

Parts Developed in the Wall of the Fore-Brain.—When a model of the fore-brain of an embryo in the 4th week of development is laid open, as in Fig. 96, it is possible to identify its two main divisions—a posterior or **thalamencephalon**, its central cavity becoming the 3rd ventricle (Fig. 96, *B*), and an anterior or **telencephalon** which will enclose the lateral ventricle. At the junction of these divisions, but yet lying distinctly in the wall of the thalamencephalon, is seen the wide evagination (Fig. 96, *A*) which gives rise to the *optic vesicle*—the basis in which the retina and optic tracts will develop. A section across the thalamic region of the fore-brain at this stage shows a right and left lateral plate, their basal margins being united by a trough-like floor plate, while their dorsal margins are joined by

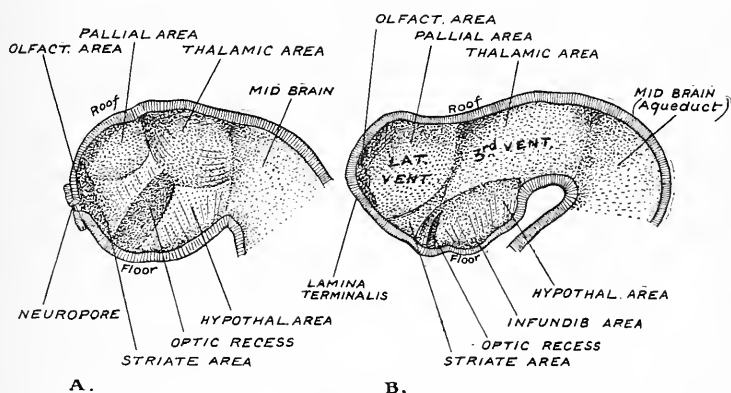


FIG. 96.—Sections of the Fore-Brain at the beginning (*A*) and near the end (*B*) of the 4th week of development.

a roof plate—which, late in the 2nd month, becomes converted into the choroid plexus of the 3rd ventricle—just as was the case with the roof plate of the 4th ventricle. The lateral plates show the usual three zones during the 4th week—an inner ependymal, in which cellular proliferation is active, a middle or mantle zone and an outer or marginal which, in the 3rd month, becomes invaded by the great trackways leading to and from the fore-brain. At this early stage, too, a groove can be seen running obliquely on the lateral wall of the 3rd ventricle, from the floor of the mid-brain to the optic recess (Fig. 96, *B*), indicating a division of the lateral plate into an upper or thalamic and a lower or hypothalamic region. In the upper region will be differentiated the **optic thalamus**, the **epithalamus** (the pineal body with its ganglia and commissures) and the **metathalamus** or geniculate bodies, while in the lower region and in the floor plate are differentiated the infundibular stalk of the pituitary body, the tuber cinereum, the mammillary bodies and the posterior perforated space. Here we are chiefly concerned with the walls of the 3rd ventricle, but it may be noted in Figs. 96, *A* and *B*, that the three areas of the telencephalon can

also be identified—the cortical or pallial area of the cerebral evagination, the striate area—forming a junctional zone between the thalamic region of the 3rd ventricle and the pallial area of the lateral ventricle (Fig. 96, *B*) and an olfactory area. At the beginning of the 4th week (Fig. 96, *A*) the neuropore is still open, and the olfactory areas which will appear at each side of the closed opening can hardly be said at this time to be differentiated.

By the end of the 6th week certain notable changes have occurred in the fore-brain (Fig. 97); the cerebral vesicle is now rapidly expanding, its hinder or occipital end beginning to expand over and cover the roof and lateral walls of the thalamencephalon. The opening of the lateral ventricle has become relatively smaller, owing to the upgrowth and more intimate fusion of the **corpus striatum** with the optic thalamus. In the hypothalamic region we can now see a recess behind the optic chiasma, indicating the outgrowth of the infundibular process of the pituitary body

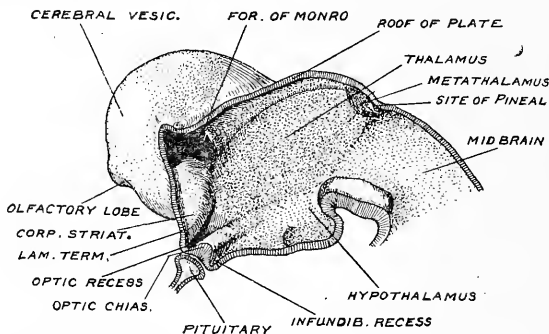


FIG. 97.—The Thalamencephalon towards the end of the 6th week of development.

(hypophysis) and growing towards it an ingrowth of ectoderm from the embryonic mouth or stomodaeum. The roof plate is now beginning to be converted into a secretory structure—the choroid plexus of the 3rd ventricle. The roof plate can be seen to extend (Fig. 97) from a slight dip or fold over the foramen of Monro to the region of the pineal body at the anterior border of the mid-brain.

In Fig. 98, which represents in a diagrammatic manner the simple fore-brain of an embryo at the end of the first month of development, there have been represented—following a scheme devised by Professor Elliot Smith—the great sensory pathways which terminate in the thalamencephalon and make it into the great court of sensory appeal. These fibre tracts, which do not begin to make their way through the mid-brain from the medulla and cord until the end of the 3rd month of development, are depicted by simple arrows—the medial lemniscus and auditory tract ending in the optic thalamus, while the gustatory tract ends in the hypothalamic region. Relays of fibres commencing in the thalamencephalon carry optic, auditory, gustatory and common sensory impulses to the telencephalon—the highest court of sensory appeal. It is when this broad conception of the relationship of the fore-brain to the sensory tracts is

grasped that we begin to understand the reason for the transformation of the simple fore-brain of the embryo into the elaborate cerebrum of the adult.

The **Lamina terminalis** forms the anterior or terminal wall of the simple fore-brain of the 4th week embryo (Fig. 96, *B*); it is completed by the closure of the neuropore (Fig. 96, *A*). When the cerebral vesicles grow out it becomes demarcated as a plate stretching from the foramen of Monro above to the optic chiasma below (Fig. 97), and joining together the olfactory areas of the cerebral vesicles. This simple plate, which comes to form the anterior wall of the 3rd ventricle, begins to assume great importance in the second month, because it serves as a bridge for the crossing of nerve tracts between the right and left halves of the telencephalon. The development of these commissural tracts will be mentioned later; in the meantime it may be pointed out that part of it retains almost its

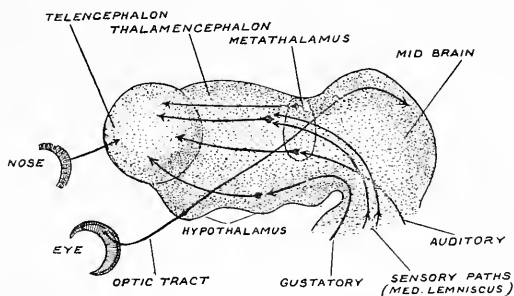


FIG. 98.—Diagram of the Embryonic Fore-Brain, to show how its various parts become linked to sensory tracts. (Elliot Smith.)

embryonic state in the adult and forms the lamina cinerea which closes the anterior wall of the 3rd ventricle between the optic chiasma below and the corpus callosum above.

Glands arising from the Walls of the 3rd Ventricle.—We have seen that the roof plate of the 3rd ventricle is converted into a secretory structure—the choroid velum. We now proceed to note the manner in which two remarkable glandular bodies arise in connection with the 3rd ventricle—the pituitary in relationship to the anterior part of its floor and the pineal from the hindmost part of its roof. We must suppose that their functions are closely related to the nutrition and welfare of the nerve system. The position and connections of these two bodies will be seen in Figs. 99, 100. A sagittal section of the pituitary body of a foetus of the 5th month is drawn in Fig. 99, showing the neural part derived from the floor of the 3rd ventricle and the buccal, derived from the ectoderm of the primitive mouth. In the buccal part the central cavity divides the glandular mass into a part applied to the neural lobe into a paraneural or intermediate and a larger anterior part or lobe. Besides these *two* parts there is a third, the lateral or tuberal part, which is seen on section in Fig. 99, applied as a plate to the neck of the infundibulum. The pineal body of a newly born child is represented in Fig. 100; it is about the size of a wheat grain,

resting on the roof of the mid-brain, between the superior corpora quadrigemina. On each side are seen the upper surfaces of the optic thalami.

Pituitary Body.—As is so often the case in the development of the human body, procedures which take place obscurely in man, present themselves with almost diagrammatic sharpness in low vertebrates—particularly in selachians, of which the dog-fish may be taken as a type.

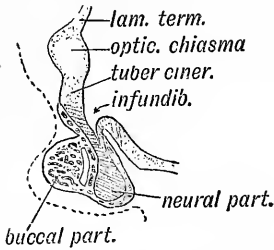


FIG. 99.—Section of the Pituitary Body of a Human Foetus in the 5th month. (Edinger.)

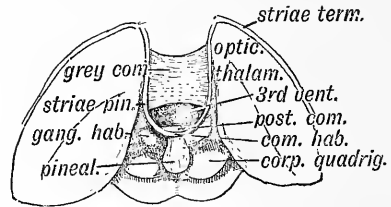


FIG. 100.—Showing the position of the Pineal Body and its commissure and ganglion.

The original saccular form of the pituitary body and its division into three parts or lobes are well seen in the pup dog-fish (Fig. 101). The original stalk is indicated, and the three parts into which the sac becomes divided by the growth and proliferation of the epithelial cells in its walls are shown. The lateral or tuberal parts arise as right and left diverticula near the root of the stalk. The tuberal part, as a distinct element of the pituitary

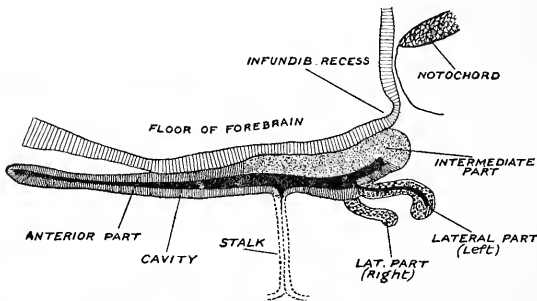


FIG. 101.—Sagittal Section of the Pituitary Body of a Pup Dog-Fish. (After Baumgartner.)

complex, was first recognized by Dr. Tilney in 1913,¹ but since then its presence has been noted in all vertebrates, including man. The lateral or tuberal parts as they expand become applied to the infundibular region of the floor of the 3rd ventricle, their cells invading the arachnoid and occupying its meshes.

¹ For recent literature relating to the development and morphology of pituitary, see Miss K. M. Parker's excellent paper, *Journ. Anat.* 1917, vol. 51, p. 181 (pituitary of Marsupials); Prof. J. E. S. Frazer, *Lancet*, 1916, vol. 2, p. 45; Dr. E. Rudel, *Anat. Hefte*, 1917, vol. 55, p. 187 (pituitary of Man); E. A. Baumgartner, *Journ. Morph.* 1915, vol. 26, p. 391; vol. 28, p. 209; W. J. Atwell, *Anat. Rec.* 1918, vol. 15, p. 73; Prof. P. T. Herring, *Journ. Exper. Physiol.* 1908, vol. 1, p. 121.

By the end of the 4th week the basis of the buccal part of the pituitary can be recognized in the roof of the primitive mouth or stomodaeum (Fig. 102, *A*), just in front of the *oral plate*, which at this time closes the anterior end of the fore-gut. The stomodaeum is lined with ectoderm, and it is therefore an ectodermal evagination, known as *Rathke's pocket*, which goes to form the buccal part of the pituitary. It will be noted that the ectodermal element is closely applied to the floor of the fore-brain from the start; in the 5th week the adjacent part of the neural floor begins to grow out, and becomes the infundibular process. One other point should be noted; just behind the upper attachment of the oral plate the entoderm of the fore-gut forms a slight pocket. *Seessel* found that in some animals (birds) this pocket also took part in the formation

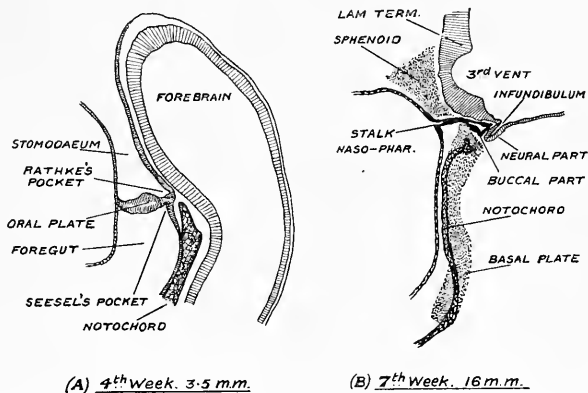


FIG. 102.—Development of the Pituitary. *A*, its condition in a Human Embryo 4 weeks old; *B*, in an Embryo in the 7th week of development. (Rudel.)

of the pituitary, and hence is called *Seessel's pocket*—it, however, does not share in the production of the human pituitary.

By the 7th week marked changes have occurred (Fig. 102, *B*). The infundibular process (the neural part) is now quite evident; its cavity is still open, becoming filled up in the 9th week. The buccal evagination has assumed a pocket form—pressing against the neural process, its neck having become drawn out into a long stalk, because the base of the skull is being laid down between the roof of the pharynx and the floor of the fore-brain. The nasal and buccal cavities are being developed, the buccal end of the stalk coming ultimately to lie at the posterior border of the nasal septum. Usually some fragments of the pituitary stalk persist in the mucous membrane on the roof of the nasopharynx; cases occur in which, owing to a malformation of the base of the skull, the whole pituitary body lies in the posterior part of the nasal septum. By the 9th week the stalk has disappeared, but occasionally a canal in the body of the sphenoid bone of the adult—the *cranio-pharyngeal canal*—marks the site of the embryonic stalk.

During the 3rd month the epithelial lining of the pituitary sac grows rapidly, particularly in the anterior part where glandular masses encroach

upon the lumen (Fig. 103), ultimately obliterating all but the central space between the anterior and intermediate parts. The gland encapsules itself in the tissues of the dura mater, branches of the internal carotids and mesodermal tissue entering the glandular masses as they begin to proliferate into the central cavity (Fig. 103).

Many theories have been framed to account for the position and formation of the pituitary in the floor of the 3rd ventricle, a favourite one being that it had been formed round the opening or mouth of the central canal of the nervous system when that canal was alimentary in nature. It seems more probable, judging from recent observations of Cushing, that the pituitary is so placed, because it discharges a secretion into the 3rd ventricle, which circulates in the cerebro-spinal fluid. Gaskell, who regarded the neural or cerebro-spinal canal as the homologue of the invertebrate alimentary canal, homologized the pituitary evagination of the buccal ectoderm with the invertebrate mouth and gullet, and the pituitary body itself with

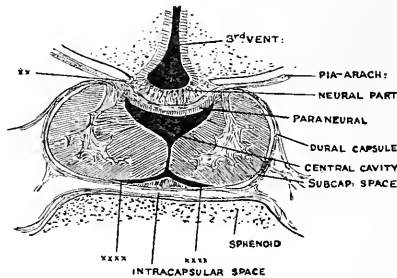


FIG. 103.—Coronal Section of the Pituitary Body of a Human Foetus at the beginning of the 4th month of development. The section is across the anterior lobe.

the coxal glands of crustaceans. The pituitary body exercises a curious influence on the growth of certain parts, especially on the face and limbs. Disease of the pituitary body may lead to overgrowth of the limbs, as in giants, or of the face, as is seen in cases of acromegaly.

Pineal Body or Epiphysis.¹—In recent years it has been shown that both pituitary and pineal bodies secrete substances which have a powerful influence on the development and growth of tissues, that of the pineal being more especially on those parts which are correlated with sexual maturity. The situation of the pineal body at the hinder end of the roof of the 3rd ventricle is shown in Fig. 100, but its connections—especially with the posterior commissure, habenular commissure and choroid plexus—are better seen in Fig. 91. Originally the **Pineal organ** was a complex structure, consisting, as is shown in Fig. 104, of a parietal organ or eye, the organ being socketed in the sagittal suture, and an adjacent glandular structure opening on the roof of the 3rd ventricle. In mammals, as in man, only the 3rd or glandular part, nerve nuclei and commissures are developed. In fossil reptiles and in some forms still living it forms a median eye which

¹ Papers on development and nature of the pineal body are: Dr. Knud Krabbe, *Anat. Hefte*, 1916, vol. 54, p. 191; A. Dendy, *Phil. Trans.* 1911, Ser. B, vol. 201, p. 227; J. Warren, *Amer. Journ. Anat.* 1911, vol. 11, p. 313.

perforates, and appears on, the dorsum of the head, between the parietal bones. It differs from the lateral eyes which grow from the third ventricle

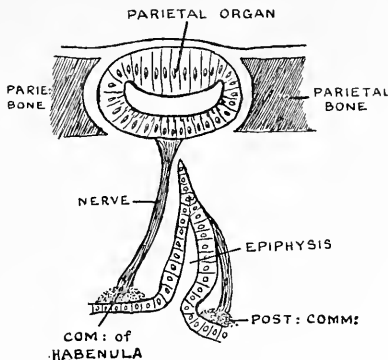
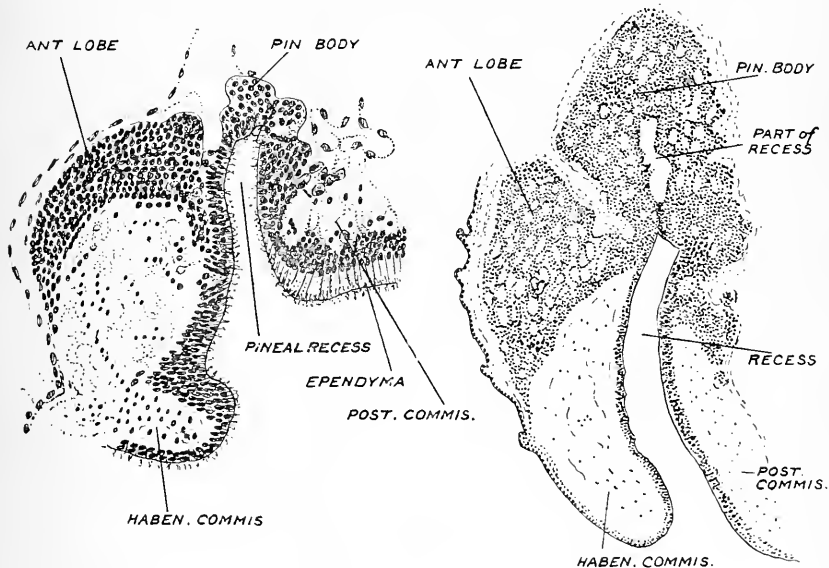


FIG. 104.—The Pineal Gland and Sense Organ in a Lizard. (Gaupp.)

as the optic vesicles in this, that it produces the lens as well as the retina and optic stalk. The retina is inverted—i.e. the apices of the rods and cones point towards the vitreous chamber. The ganglion of the habenula,



(A) 3rd MONTH.

(B) 6th MONTH.

FIG. 105.—Showing stages of development of the Pineal Body in the roof of the Fore-Brain: A, in the 3rd month; B, in the 6th month. (After Krabbe.)

situated on the dorsal and inner aspect of the optic thalamus, appears to represent its terminal ganglion, but it must also be remembered that this ganglion receives the striae pinealis which arise from part of the rhinen-

cephalon. The two ganglia become connected across the roof plate by a commissure (the superior or habenular commissure) (Fig. 100).

The manner in which the pineal body arises in man is shown in Fig. 105. At the posterior end of the roof of the fore-brain the ependymal lining grows out as a pocket in the 6th week of development. The evaginated cells form a zone for cellular production (Fig. 105, *A*), as we have seen is the case everywhere in the neural tube, but in this instance the cells produced are mainly glandular in nature, there being, however, as Dr. Krabbe has observed, also some neuroglial and neuroblastic elements. From the anterior wall of the pocket a mass of cells separates early to form an anterior lobe (Fig. 105). In the sixth month (Fig. 105, *B*) the body is assuming its final form; part of the recess or pocket has become closed off in the distal part of the gland. The glandular masses are invaded by vascular and mesenchymal tissue, and the same formation of interlacing columns is produced as is seen in the buccal part of the pituitary or cortical part of the adrenals. How this body has become associated with the development of the sexual system is an enigma.

CHAPTER X.

THE FORE-BRAIN OR PROSENCEPHALON (*continued*).

CEREBRAL VESICLES.

WE are now to follow the development of the organ which has given men the domination of the world—the cerebrum proper, comprising the right and left cerebral hemispheres. Nothing could be simpler than the cerebral vesicles at the end of the 1st month of development; they are merely button-like bulges on the right and left walls of the fore-brain (Fig. 96). Each button-like vesicle may be demarcated into three areas—a relatively small olfactory area in front, which will be evaginated to form the *olfactory vesicle*, afterwards converted into the olfactory bulb and tract; a *striate area* in which that great basal mass of nerve nuclei, known as the *corpus striatum*, will be developed; and a *pallial* or *mantle* area in which the cortical centres, which make up the great mass of the cerebral hemispheres, are produced. In each vesicle there is also a fourth or *secretory area*, which, however, does not become defined until the middle of the 2nd month, when it is folded within the cavity of the vesicle to form the glandular covering of the choroid plexus of the lateral ventricle.

It is important to note the manner in which the cerebral vesicles are connected to the walls of the 3rd ventricle and to each other. At what may be called its posterior border each vesicle is continuous with the optic thalamus (Figs. 96, 97); at its lower border, with the hypothalamic region. At both of these borders it is the striate area which joins with the thalamic regions; nerve tracts which arise in the nuclei of these regions and pass to the mantle areas must traverse the striate zone; there is no other route. Hence the corpus striatum becomes the bond which links each cerebral vesicle to the thalamencephalon; it becomes the highway for the *internal capsule*, the name given to the great afferent and efferent nerve-tracts which link the lower nerve centres to the cortex and the cortex to the lower centres.

Having thus examined the connections of the cerebral vesicles along their posterior and inferior borders, we now turn to the remaining two—the anterior and superior borders (Figs. 96, 97). Along the anterior border one cerebral vesicle is united to the other by the *lamina terminalis*, which, we shall see, becomes enormously distorted by the development within it of, (1) the anterior commissure, (2) the hippocampal commissure and (3) the corpus callosum (see Figs. 116, 117, 118). Along the superior

border the vesicles are united by a roof plate; posteriorly the vesicular roof plate is continuous with the roof plate of the 3rd ventricle, which at the 6th week becomes transformed into choroidal ependyma (Fig. 108). A similar change affects the vesicular roof plate and a neighbouring area of the vesicular wall to form the *velum interpositum*. The vesicular roof plate lies over the widely gaping orifice of the cavity of the cerebral vesicle (Fig. 96). By the end of the 6th week (Fig. 97) the expansion of the cerebral vesicles has commenced; we can then name the cavity of each vesicle—*lateral ventricle*, and its constricted communication with the 3rd ventricle, the *interventricular opening* or *foramen of Monro*.

Expansion of the Cerebral Vesicles.—By the middle of the second month the rapid expansion of the cerebral vesicles has commenced, as may be seen in Fig. 106. Already the posterior or temporal region is passing backwards and downwards on the side and roof of the thalamencephalon (Fig. 107); the frontal region is bulging forwards over the olfactory bulb,

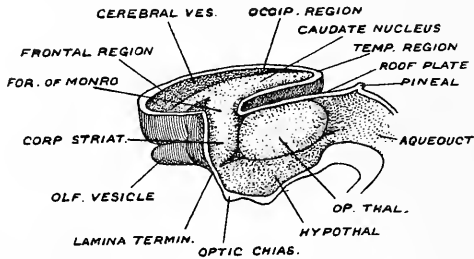


FIG. 106.—The expansion of the right Cerebral Vesicle and the formation of the Corpus Striatum on its floor, during the 6th week of development.

while the roof of the vesicle, which is cut away in Fig. 106 to expose the corpus striatum in the floor, is rising up so that between the right and left vesicles there now exists a fissure—the commencement of the *longitudinal fissure*, which will become deeper and longer as the vesicles expand. We have already seen that the striate area of each vesicle is continuous with the thalamic areas of the fore-brain, and thus as the corpus striatum becomes differentiated it is continuous with the optic thalamus (Fig. 106), and hence this striate-thalamic junction may be looked on as the stalk or hilum from which the cerebral expansion takes place. The corpus striatum occupies the floor of the vesicle, so that in the fully formed brain we find the caudate nucleus stretching along the lateral ventricle from the foramen of Monro to the end of the descending horn which represents the posterior or caudal pole of the embryonic brain.

It is also instructive to note the expansion of the cerebral vesicle as seen on its lateral aspect (Fig. 107). At the 6th week the bean-shaped vesicle still leaves the greater part of the thalamencephalon exposed (Fig. 107); it then shows only a frontal and temporal pole, but by the end of the 3rd month, the expansion has reached the mesencephalon, and now there has appeared a third or occipital pole (Fig. 107, B); by the end of the 5th month the occipital region overlaps and covers the hind-brain. On embryological grounds alone one could infer that the dominance of the cerebrum

is one of the more recent products of evolution. In the lateral aspect we again see how the corpus striatum forms the basis or fixed area from which the cerebral expansion is produced. The three primary constituents of the cerebral vesicle are indicated in Fig. 107, *A*, the small olfactory area, the large mantle formation and the position of the striate element at the junction of these two. The position of the corpus striatum determines the non-expansion of the overlying cortex—which later becomes differentiated to form the Island of Reil. The position and relationships of the islandic region towards the end of the 3rd month are shown in Fig. 107, *B*.

The Velum Interpositum.—It is during the growth backwards of the cerebral hemispheres over the thalamencephalon that the basis of that complex structure—the velum interpositum—is formed. The basis of this structure is really that area of the pia mater—the mesodermic and vascular

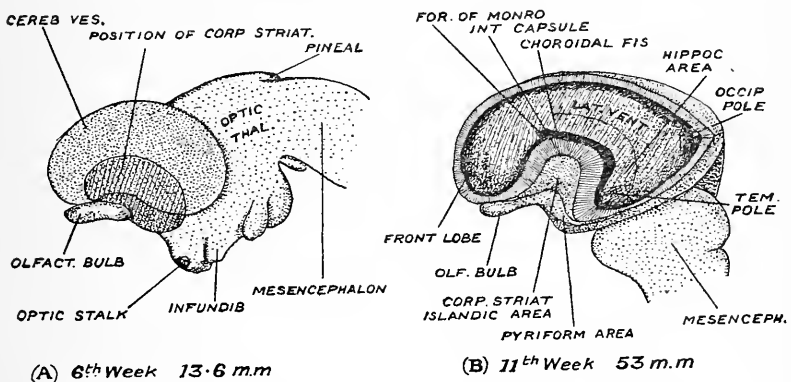


FIG. 107.—The Expansion of the left Cerebral Vesicle as seen on its lateral aspect. *A*, at the 6th week; *B*, at the 11th week; in *B*, a window has been cut to expose the lateral ventricle, the corpus striatum and the choroidal gap. (After His.)

capsule of the brain—which is enclosed between the thalamencephalon and expanding cerebral vesicles (Fig. 108). The essential parts of the velum are its lateral edges, which project within the lateral ventricles and its lower surface lying over the third ventricle—parts which are covered by reflections of those areas of the neural tube which have been converted into a glandular or secretory epithelium. These parts form the choroidal villi—or plexuses—covered by the ependymal epithelium, which secrete the cerebro-spinal fluid.

We have seen that in the anterior part of the roof plate of the 4th ventricle the cerebellum is developed, while its posterior half becomes the inferior medullary velum—a secretory membrane (Fig. 86, p. 91). The roof plate of the third ventricle, from the foramina of Monro backwards to the stalk of the pineal body, becomes modified in a similar manner (Fig. 108). It merely forms the ependymal covering of the lower surface of the velum interpositum, thus clothing the choroid plexus on the roof of the 3rd ventricle (Fig. 109). The anterior part of the roof plate is produced into the cerebral vesicles at the foramina of Monro, and covers the apex of the velum

interpositum (Fig. 108). The mesial wall of each cerebral vesicle from the foramen of Monro back to the posterior extremity of the vesicle (Figs. 108, 109), which becomes the tip of the descending horn, is also inflected and forms a secretory ependyma, covering the velum interpositum and choroid plexus within the lateral ventricles. Into this inflection—the **choroidal fissure** of the embryonic neural wall—spreads the mesoderm, carrying vessels with it. The velum interpositum is thus composed of a basis of mesoderm, while its intraventricular parts have an ependymal

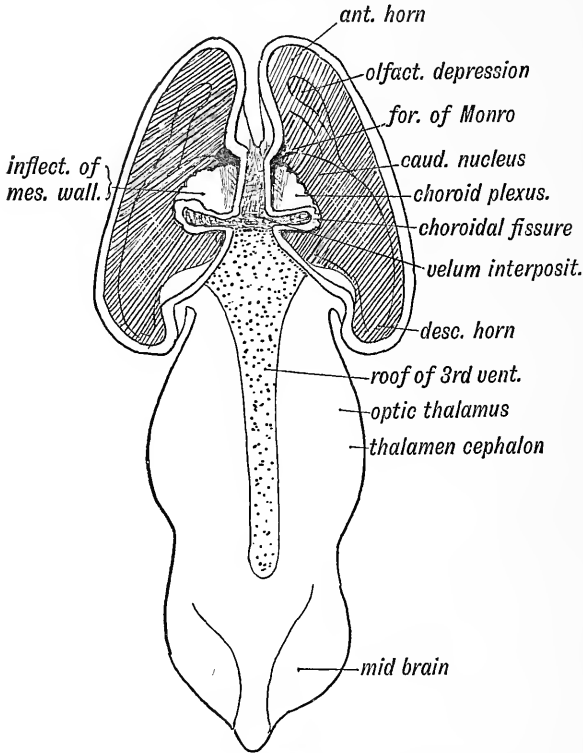


FIG. 108.—A dorsal view of the Fore- and Mid-Brain at the 6th week of development to show the formation of the Velum Interpositum. The Cerebral Vesicles are laid open and the inflection of the roof of the Fore-Brain shown on the ingrowing Velum. The Roof Plate of the 3rd Ventricle is also exposed. (Modified from His.)

covering derived from the neural wall. When the velum interpositum is withdrawn from the foetal brain (Fig. 107, *B*) a linear opening is seen extending from the foramen of Monro to the temporal end of the cerebral vesicle.

The ependymal covering of the entire velum is derived from :

- (1) The roof plate of the 3rd ventricle (lower surface) ;
- (2) The roof plate of the foramina of Monro ;
- (3) An inflection of the mesial wall of the cerebral vesicle.

The choroid plexus, which merely fringes the velum in the adult, completely fills the cavities of the embryonic lateral ventricles. These for the

first three months are relatively very large and their containing walls thin. The velum and choroid plexus must play an important part in the development of the cerebral vesicle in the early period of growth. The spread of the vesicles backwards and downwards over the optic thalami obscures the original simple relationship of the velum to the brain; but, when withdrawn from the transverse fissure, the velum is seen to rest on the optic thalami and project within the ventricle from the foramen of Monro to the tip of the descending horn. This stretch marks the line at which the choroidal inflection took place (Fig. 109). The taenia semicircularis, in the groove between the optic thalamus and caudate nucleus (Fig. 100), marks the line at which the mesial wall of the cerebral vesicle was primarily attached.

The fibrous substance of the velum interpositum is continuous with the pial covering of the brain, and also with the edge of the tentorium cerebelli,

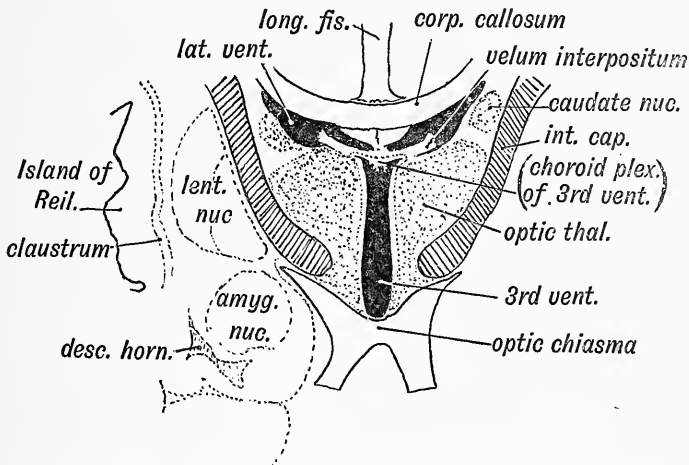


FIG. 109.—Diagrammatic Section across the 3rd and lateral Ventricles of the Adult to show the Structures formed in their Walls.

for as the cerebral vesicles expand not only do they evaginate their proper mesodermal covering, the pia-arachnoid, but also the inner or dural stratum of the primitive cranial capsule. The corpus callosum and cerebral vesicles, as they develop, grow backwards and enclose, between the optic thalami below and the pillars of the fornix above, the fibrous basis of the velum interpositum (Fig. 109). The veins of Galen are developed in the velum and join the straight sinus in the tentorium.

Corpus Striatum.—When a coronal section is made of the adult brain (Fig. 109) to expose the connections of the velum interpositum, it is clear that a mere overgrowth of the cerebral vesicles will not account for all the relationships shown. We shall see that the development of the commissures—particularly of the fornix and corpus callosum—introduces elements not seen in the simple brain of the embryo; but, besides the commissural, another change has come about in the relationship of the corpus striatum to the optic thalamus. So intimate and extensive has

the union between them become that the corpus striatum now forms a cap upon the lateral aspect of the optic thalamus (Fig. 109). Although developed in the wall of the cerebral vesicle the lenticular nucleus of the corpus striatum, and the islandic cortex are now constituents of the lateral wall of the 3rd ventricle—the cavity of the original thalamencephalon (Fig. 109). The intimate union of the corpus striatum with the optic thalamus we must regard as the result of two developmental processes: the formation of the nerve tracts of the internal capsule—which begin to appear in the 3rd month—and the neurobiotactic attraction which exists between the neuroblastic centres of the two great basal ganglia.

Two figures (Figs. 110, *A*, *B*) taken from a recent paper by Professor Elliot Smith¹ throw a new light on the nature and origin of that complex

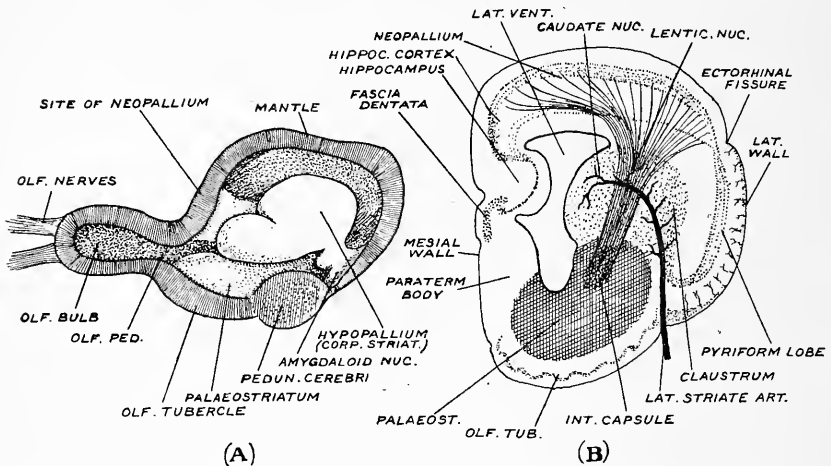


FIG. 110, *A*.—Sagittal Section of Turtle's Cerebral Vesicle made along the mesial plane so as to expose the cavity of the vesicle—the lateral ventricle. (Elliot Smith.)

FIG. 110, *B*.—Coronal Section of a Primitive Mammalian Cerebrum, made across its anterior part, in front of the 3rd ventricle, to show the origin of the constituents of the Corpus Striatum. (Elliot Smith.)

product of the cerebral vesicle—the corpus striatum. When the cerebral hemisphere of a turtle's brain is laid open, as in Fig. 110, *A*, we see the same three elementary parts as in the cerebral vesicle of the human embryo: (1) the hollow olfactory bulb, containing an extension of the ventricular cavity, (2) a mass occupying the floor and lateral wall representing the corpus striatum, (3) the vesicular wall, mantle or pallium. We see that the basal mass is made up of three projections, (1) the hypopallium representing for the greater part the caudate nucleus; (2) at its hinder or temporal end the amygdaloid nucleus; (3) the oldest part of all lying over the olfactory bulb (Fig. 110, *A*), and continuous with the hypothalamic region—the palaeostriate body. From Fig. 110, *A*, it is clear that the corpus striatum has a close connection with the olfactory region of the cerebral vesicle. The coronal section in Fig. 110, *B* shows the relationship

¹ *Journ. of Anat.* 1919, vol. 53, p. 271.

of the corpus striatum to the remaining parts of the wall of the cerebral vesicle of a primitive mammal—the type of organ from which the human cerebrum has been evolved. An artery—the lateral striate¹—one of the perforating branches of the anterior cerebral, is seen to enter the wall of the brain between the pyriform lobe above and the olfactory tubercle below and end in the corpus striatum. At the point where the artery enters, the cortex of the pyriform lobe is also inflected, although no fissure is present, and forms a stratum—the claustrum—on the outer aspect of the basal mass (Fig. 109). The cortical stratum, after forming the claustrum, bends inwards to become continuous with the nuclei of the corpus striatum. On the mesial wall of the vesicle (Fig. 110, *B*) the *hippocampus* arises in a somewhat similar way—by an inward growth of a cortical stratum—without the production of an open fissure. Elliot Smith, therefore, regards the corpus striatum as a cortical derivative; growth has taken place towards the cavity of the ventricle tending to fill up the cavity with a cortical product. In the bird's brain the cortical growth is chiefly intra-ventricular.

The Mantle or Pallium.—We have followed the fate of the striate area of the embryonic cerebral vesicle; the differentiation of the olfactory area will be dealt with when we come to consider the nose and sense of smell; there remains for consideration the third or pallial area of the cerebral vesicle. Even up to the end of the 3rd month the pallial wall of the vesicle remains thin; it then measures only about one millimetre in thickness. Originally the pallial wall shows the same three strata or zones as were seen in other parts of the neural tube—namely an inner or ependymal zone, in which neuroblasts are produced; a middle or mantle zone in which they are differentiated and an outer or marginal zone (Fig. 111). In the spinal cord the masses of neuroblasts were differentiated

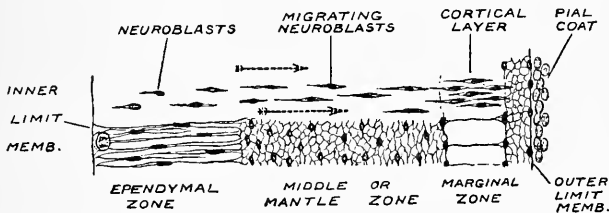


FIG. 111.—Diagram to show the differentiation of the Pallial Wall of the Cerebral Vesicle. (After His.)

within the middle zone, where they remained, but in the cerebellum—and the same is true of the pallial wall—they invade the marginal zone. It is within the neuroglial scaffolding of the marginal zone that the grey cortical matter of the cerebral hemispheres is formed. In the 2nd month the migration of the neuroblasts to form a cortical layer has already commenced; the process is particularly active in the 3rd and 4th months. Not only is there a migration from the ependymal to the marginal layer, but the production is particularly abundant where the mantle joins the corpus

¹ See paper by Col. J. L. Shellshear, *Journ. of Anat.* 1921, vol. 55, p. 27.

striatum. The middle zone, which contains grey matter in the spinal cord, is here the highway for the fibres developed from the cortical cells; it forms the white medullary mass of the cerebral hemispheres.

Evolution of the Neopallium.¹—Nothing could be more humble than the origin of man's master organ; it was evolved in connection with the sense of smell. The cerebral hemispheres, as we know them in the lowest vertebrates, are for the reception and interpretation of impulses from the olfactory end organs. Connections are established between the olfactory brain and the motor centres in the cord and in the hind- and mid-brain; olfactory impressions can thus lead to action. Further, it became advantageous that there should be a nervous mechanism for the blending of impressions from the nose with impulses derived from sight, hearing and touch, and hence there arose connecting tracts by which stimuli streaming in from the various senses could be combined and their reactions co-ordinated with those streaming in from the nose. In the stem of vertebrates which became mammalian the supreme co-ordinating mechanism

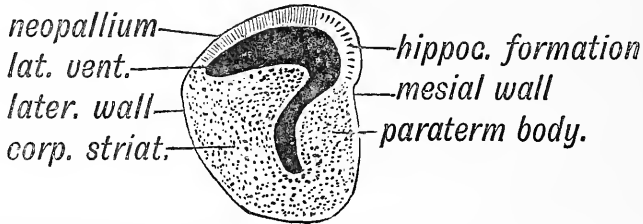


FIG. 112.—Section across the Left Hemisphere of the Brain of a primitive vertebrate brain anterior to the Lamina Terminalis, to show the small extent of the Neopallium and the relatively great development of the Corpus Striatum and Rhinencephalon. (After Elliot Smith.)

was evolved in that part of the neural system connected with smell—the telencephalon.

In Fig. 112 is represented a diagrammatic section across the anterior part of the cerebral vesicle of one of the lower vertebrate types—such a one as we may suppose preceded the modern mammalian form of cerebral hemisphere. There is a cavity within it—the lateral ventricle. The inner or mesial wall is formed of two parts: (1) the hippocampus or hippocampal formation—true cerebral cortex or mantle; (2) below the hippocampus, the paraterminal body—a nuclear mass connected with the hippocampal formation by nerve tracts. The lateral or outer wall of the primitive hemisphere is made up of two parts—the corpus striatum—a nuclear mass partly covered by the cortex of the pyriform lobe (see Fig. 110, *B*). The pyriform lobe receives fibres from the outer root of the olfactory tract. These four parts—hippocampus, paraterminal body, pyriform lobe, corpus striatum—are connected with smell, and form the primitive mantle (archipallium) of the brain. In the roof of the ventricle an expansion of the mantle appears between the hippocampal formation on the inner side and the pyriform lobe on the outer side (Fig. 117); to

¹ See Prof. Elliot Smith's "Arris and Gale Lectures," *Lancet*, 1910, Jan. 1st, 15th, 22nd.

this expansion Elliot Smith, whose account is followed here, gave the name of neopallium. It is this new mantle which becomes the basis for the higher combination of the sensory impressions coming in from all the organs of sense. It becomes the seat of consciousness and memory, and in man assumes enormous proportions; hence the great and rapid expansion of the cerebral vesicles in the human foetus.

As may be seen from Fig. 117 the primitive mantle—all the cortical formation directly connected with the sense of smell—is arranged around the peduncular attachment, which may be described as the cerebral hilum. In Fig. 118 is shown how greatly the distribution of the primitive mantle is altered when the great commissures become developed.

Projection Fibres to the Neopallium.—A transverse section of a mammalian brain of a primitive type—made further back and in a more advanced stage of development than that represented in Fig. 112—is shown

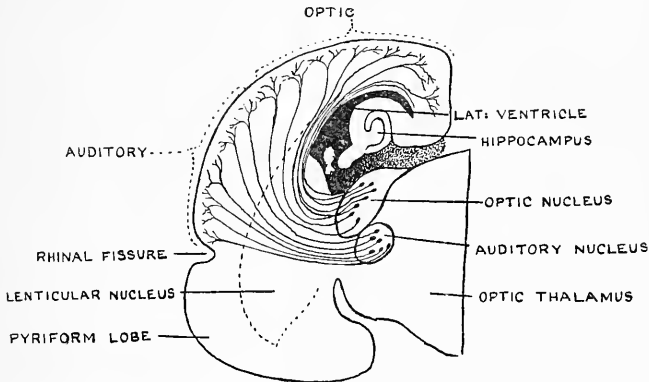


FIG. 113.—Coronal section of the right half of the Cerebral Vesicle of a Primitive Type of Mammal, showing the termination of projection fibres arising in the optic thalamus, in the neopallium. (Elliot Smith.)

in Fig. 113. The section illustrates the manner in which projection fibres arise from two of the sensory nuclei in the optic thalamus—those connected with the nerves of sight and of hearing—and spread outwards into the neopallium—each set streaming into the area which lies nearest to it. In this way the mantle of the telencephalon becomes a higher sensorium for the reception, blending and storing of all sensory impressions. Other illustrations of the cortical afferent tracts are given in Figs. 98 and 110, *B*.

Localization of Function in the Neopallium.—In Fig. 114 the brain of a primitive mammal is represented on its lateral aspect. The major part is seen to be made up of pyriform lobe, olfactory bulb and tubercle, all of them parts of the rhinencephalon. The rhinal fissure marks the junction of the neopallium with the older parts of the mantle on the outer or lateral aspect of the hemisphere. The areas adjacent to the various nuclei of the optic thalamus receive projection fibres from these nuclei. Thus it comes about that the lower and most posterior part of the neopallium, which forms the basis of the temporal lobe, receives fibres from

the auditory centre; in the upper posterior part the fibres from the optic nuclei end; this area becomes the main part of the occipital lobe. Anterior to these two areas terminate the projection fibres connected with the sensory nuclei of the Vth nerve and with the nuclei of common sensation—receiving impulses from the leg, trunk, arm and head. Hence the

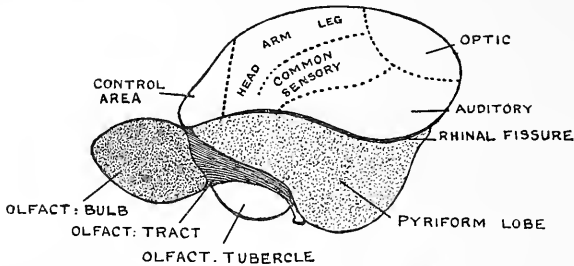


FIG. 114.—Lateral Aspect of the Cerebrum of a Primitive Mammal to show the Rhinal Fissure which separates the Neopallium above, from the older parts of the mantle below, represented by the Pyriform Lobe. The areas of the Neopallium in which the projection tracts from the optic thalami terminate are also shown. (Elliot Smith.)

surface areas of the body are represented in the neopallium. Naturally it is in connection with this area—the area of common sensation—that the cortical fibres which control the lower somatic motor nuclei arise. Anterior to the motor areas—occupying the region of the frontal pole—is an area connected with the control of the higher centres. These are the primary

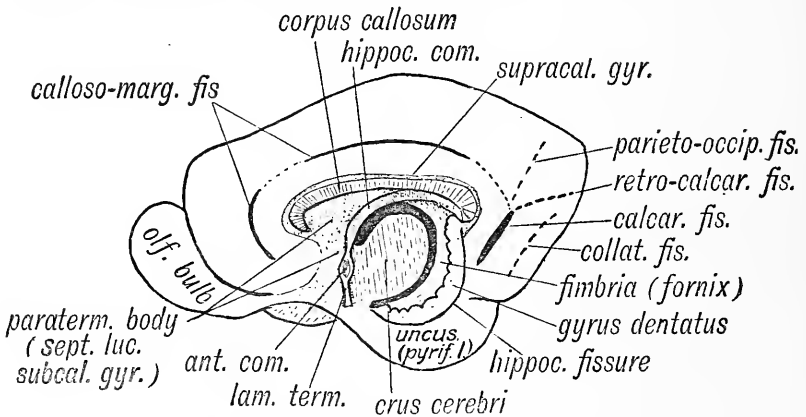


FIG. 115.—The Anterior, Hippocampal and Callosal Commissures, with the primary fissures on the Mesial Aspect of a typical Mammalian Cerebrum. (Elliot Smith.)

areas of the neopallium. In the course of evolution, secondary or associated zones have appeared round the primary areas, separating them widely and giving rise to the great mass of the human cerebrum.

Development of Cerebral Commissures.—In order to secure a co-ordinated action of the whole brain, it is necessary not only that the cerebral centres of each hemisphere should be linked up by association and projection fibres, but that the centres of one hemisphere should be

united by transverse or commissural tracts with the corresponding centres of the other hemisphere. The lamina terminalis (see Figs. 97, 116, 117) affords a natural bridge for the formation and passage of the commissures. In the most primitive vertebrates, in all of which the cerebral hemispheres are chiefly olfactory in nature, the anterior commissure is already present. The next to appear is a dorsal or hippocampal commissure which unites the hippocampal areas on the mesial surfaces of the cerebrum (Figs. 115, 117). The last and greatest to be formed is the corpus callosum; it appears in the true mammals—not in the monotremes and marsupials. Its development is commensurate with the size of the neopallium; hence it is largest in man.

The cerebral hemispheres are thus connected by fibres which cross in the lamina terminalis, and form three commissures. (1) The **anterior** or

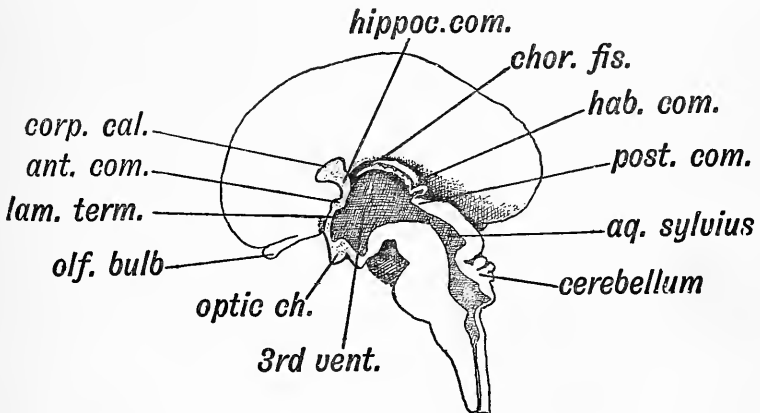


FIG. 116.—Mesial Aspect of the Brain of a Human Foetus in 4th month of development, showing the Lamina Terminalis and positions at which Commissures are formed. (After Goldstein.)

ventral commissure, which connects the olfactory tracts, and afterwards parts of the temporal lobes; (2) the **dorsal** or **hippocampal** commissure also formed in the lamina terminalis; in man this commissure becomes the fornix; (3) the **corpus callosum**, which unites the neopallium of one side with that of the other. It is formed in the lamina terminalis above the dorsal or hippocampal commissure (Figs. 114, 115, 116). The **middle** or grey commissure (Fig. 100) is merely an adhesion between the ependymal coverings of the optic thalami; the **optic chiasma** (p. 207), the **habenular** or superior commissures (p. 110) need only be again mentioned. The **posterior commissure** is formed in the roof plate at the junction of the mid- and fore-brains (Figs. 94, 100).

(1) **The Anterior Commissure** (Figs. 116, 117) is developed in the lamina terminalis—the primitive anterior wall of the fore-brain. The commissure crosses in the lamina terminalis below and rather anterior to the foramen of Monro.

(2) **Hippocampal Commissure**.—Four parts are recognized in the fornix of the human brain (Fig. 118): (1) the body, adherent to the under

surface of the corpus callosum; (2) the posterior pillars, which are continuous with (3) the fimbriae and fibres of the alveus, covering the ventricular aspect of the hippocampus; (4) the anterior pillars which end in the corpora mammilaria and optic thalami. The fornix contains two systems of fibres: (1) those which cross in the body and connect the hippocampal

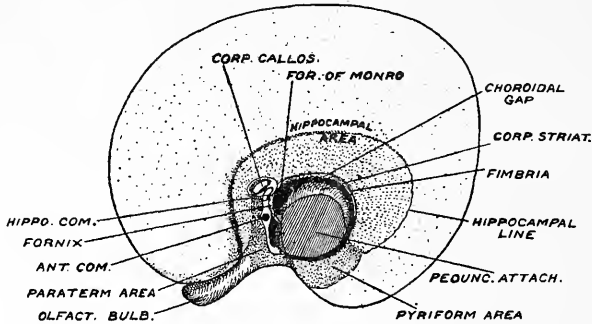


FIG. 117.—Mesial aspect of the Cerebral Vesicle of a Foetus about 3 months old, showing the commissures developing in the lamina terminalis and the distribution of the cortical areas which belong to the rhinencephalon. (After Streeter.)

cortex of one side with that of the other, and form the true dorsal or hippocampal commissure, (2) fibres which connect together the various parts of the rhinencephalon of the same side, and with the corpora mammilaria and optic thalami.

To understand the development of this system it is necessary to obtain a clear conception of the relationships of the lamina terminalis to the

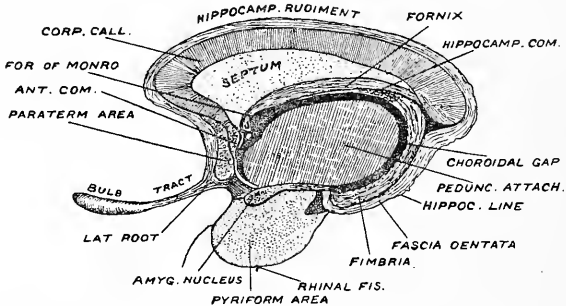


FIG. 118.—Diagram to show the structures formed in the Lamina Terminalis and Primitive Callosal Gyrus. (After Elliot Smith.)

various parts which have been distinguished in the rhinencephalon (Figs. 115, 117). On each side the lamina terminalis is continuous with the **paraterminal body**—that part of the rhinencephalon which lies immediately in front of the lamina terminalis. The paraterminal body becomes the subcallosal gyrus and septum lucidum in the mature brain (Fig. 118). The hippocampal formation, which includes the hippocampus and fascia dentata, bounds the choroidal fissure above (Figs. 117, 118). Fibres

developed in the hippocampal formation cross to the opposite side in the lamina terminalis above the anterior or ventral commissure, thus forming the **dorsal commissure** (Fig. 116). It becomes included in the body of the fornix. The posterior pillar is developed in the hippocampal cortex, which forms the lip of the choroidal fissure. The anterior pillar lies in the paraterminal body and lamina terminalis.

(3) **Corpus Callosum.**—The corpus callosum is the commissure of the **neopallium**, and hence in man, in whom the neopallium forms by far the greatest part of the cerebrum, this commissure attains an enormous development. The commissural fibres begin to form towards the end of the third month, crossing in the lamina terminalis with the fibres of the hippocampal commissure, but situated on their upper or dorsal aspect (Figs. 116, 117). As the corpus callosum rapidly increases within the lamina terminalis, it presses backwards on the hippocampal formation, and forwards on the paraterminal body. The hippocampal commissure is stretched, and forms the body and anterior pillars of the fornix. The hippocampal formation becomes (1) the supra-callosal gyrus, the hippocampus and fascia dentata (compare Figs. 117 and 118). The velum interpositum is overwhelmed and buried during the growth backwards of the corpus callosum and fornix. The paraterminal body is stretched to form the septum lucidum and subcallosal gyrus (Fig. 118). Thus by the development of the corpus callosum those two parts of the rhinencephalon—the paraterminal body and hippocampal formation—originally in close union, become widely separated. The supra-callosal and subcallosal gyri are vestiges of their former union. The corpus callosum may not be developed—a rare occurrence; it is remarkable that this condition cannot be detected during the life of the individual.¹

Formation of Fissures.—Until the 5th month the surface of the cerebral vesicle is comparatively smooth. Up till then the three strata of the cerebral vesicle, the ependymal layer within, the cortical or nerve-cell layer on the surface and the medullary or nerve-fibre layer between, have increased at an equal rate. In the 6th and 7th months certain areas of the cortex increase rapidly, the increase affecting the superficial area to a very much greater extent than the deep, and affecting the cortex much more than the medulla, with the result that the surface of the cerebrum becomes raised into certain definite eminences or gyri, separated by depressions or fissures. The chief fissures are already well differentiated in the foetus of the 7th month; during the last two months of intra-uterine development the secondary and tertiary sulci appear. The process of fissuration and convolution-formation are thus practically finished at birth. In the spinal cord the tracts of nerve fibres are formed outside the masses of grey matter; in the cerebral vesicle the tracts are formed beneath the grey matter—between the grey matter and the ependyma (see p. 80). The neuroblasts in the cortex have reached nearly their full number by the 7th month; after then it is their dendrites and collateral fibres that continue to develop (His).

¹ See cases described by Elliot Smith and by Cameron, *J. Anat. and Physiol.* 1907, vol. 41, pp. 234, 293.

Development of the Cortex.—The mantle or wall of the cerebral vesicle of the brain becomes differentiated into a thin outer grey layer or cortex, containing the nerve cells, and an inner deep stratum—the medulla—of great thickness and made up of nerve fibres and tracts associated with the nerve cells of the cortex. The cortex is the substratum of consciousness, memory and mind. We naturally expect the great mental development which takes place in the earlier years of life to be accompanied by a corresponding change in the microscopic structure of the cortex. There is such a change, but it is difficult to measure for two reasons: (1) every area of cortex has its own peculiar structure and thickness; Elliot Smith¹ has distinguished 28 areas in the cortex, each having its own peculiar structure; (2) Dr. Joseph Bolton² observed that in some cases a newly born child may show a more mature development than a child of 3 months, there being as much variation in structure of cortex as in degree of ability. The latter observer noted that the cortex began to laminate or divide into three strata of nerve cells at the beginning of the 6th month, when the fissures and convolutions are in process of formation. He also made the important observation that the outer or pyramidal stratum was the latest in growth, and that the great development of this layer is the characteristic of the human cortex.

The Principal Fissures.—The principal fissures of the brain are: (1) those connected with the rhinencephalon—the rhinal fissure (Figs. 114, 118) and the pseudo-hippocampal fissure—a mere linear depression (Elliot Smith); (2) those connected with the isolation of the Island of Reil—the fissure of Sylvius, the superior, inferior and anterior limiting fissures; (3) those in the occipital cortex connected with the sense of sight—the calcarine, retro-calcarine, lunate sulcus (Affenspalte) parieto-occipital and collateral, (4) the calloso-marginal of uncertain import, (5) the fissure of Rolando, which is formed between motor and sensory areas of the cortex, (6) the orbital, (7) the sulcus rectus, (8) the intra-parietal, (9) the 1st temporal or parallel, which partially demarcates the auditory cortex. In the 7th month the fissures on the human brain have a remarkable correspondence to those on the cerebrum of an ape (Figs. 121, 123). We have already seen that the so-called **choroidal fissure** is formed by an inflection of the vesicular wall to form the choroidal villi of the lateral ventricles (Fig. 108).

Significance of Convolutions.—There is some circumstance which limits the thickness of the cortex. If the cortical cells increase in number, accommodation is obtained, not by adding to the thickness of the cortex, but by enlarging the superficial area of the cerebrum. The cortex is correlated in its extent with the bulk of the body and with the area of the integumentary covering. Hence large animals such as whales and elephants have much convoluted brains. The rich convolutions of man's brain may be in some degree related to the nude and sensitive skin of his body (Elliot Smith). The most satisfactory explanation of the number and arrangement of the convolutions of the human brain is to be found in

¹ Prof. Elliot Smith, *Journ. of Anat. and Physiol.* 1907, vol. 41, p. 237.

² Dr. Joseph S. Bolton, *Brain*, 1910, vol. 32, p. 26.

a study of the evolution of its various functional areas. The cortex was originally composed of primary sensory areas—connected with sight, touch, hearing, smell, etc. When secondary and higher zones were produced in connection with the primary areas, the surface of the brain was necessarily thrown into folds and fissures to provide the increase of surface required. Hence we find that the principal fissures are distinctly related to certain cortical areas. Elliot Smith distinguishes three kinds of fissures: (1) those like the calcarine and central fissures which separate one cortical area from another (being *limiting* fissures or sulci); (2) those like the lunate (Fig. 126), where the line of cortical demarcation lies, not at the bottom of the fissure, as in the last, but at the brink of the fissure. These are named **operculate**, because the convolution or operculum, which causes the fissure or depression, arises at the junction of two areas; (3) a developing area may fold inwards, thus giving rise to a depression in the centre of an area, like the retro-calcarine in the midst of the visuo-sensory area (Fig. 127). The hippocampal linear depression and Sylvian fossa,

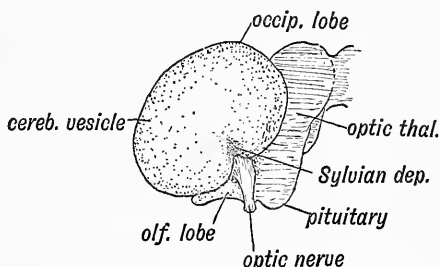


FIG. 119.—Lateral Aspect of the Cerebral Hemisphere at the end of the 2nd month.

as we have already seen (pp. 113, 117), are peculiar in their formation. Two fissures—the retro-calcarine and the collateral—actually cause an infolding of the whole thickness of the mantle, and give rise to two elevations in the posterior and descending horns of the lateral ventricle.

Formation of the Island of Reil and Fissure of Sylvius.—When the lateral wall of the cerebral vesicle is examined at the 5th month (Fig. 120) an area of cortex is seen to be rapidly becoming submerged by the overgrowth of the surrounding cortex. The submerged area is the Island of Reil; it covers that part of the wall of the cerebral vesicle which is thickened by the corpus striatum (Figs. 107, *B*, 109). The submerged area becomes triangular in shape, the apex being directed backwards; it is bounded by three **limiting sulci**—an anterior, superior and inferior. The rising lips of cortex, which bound the limiting sulci, form the temporal, fronto-parietal and orbital opercula, and ultimately meet over the submerged area (Fig. 122). The fissure of Sylvius separates the opercula. It will be readily grasped that the development of the corpus striatum prevents the expansion of the insular part of the vesicle, whereas the thin-walled mantle, out of which the other lobes of the brain are developed, expands readily and overwhelms the thickened area. The corpus striatum begins to form during the 2nd month, hence as early as that date the

insular depression is visible on the lateral wall of the hemisphere (Fig. 119). This mechanical explanation of the origin of the fissure of Sylvius is probably only partially true; the relatively great growth of the cortex which forms the opercula is due in the main to its great functional importance. By comparing Figs. 119 and 121 it will be realized that the formation of the

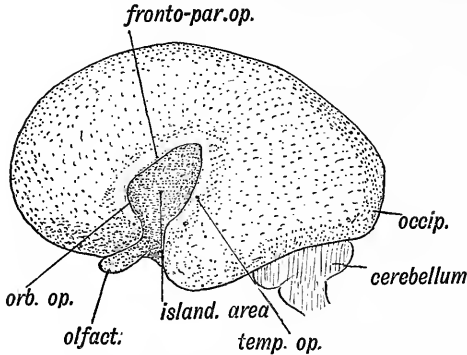


FIG. 120.—The same Aspect during the 5th month.

Sylvian fossa is connected with the expansion and downward growth of the temporal lobe. The growth of the temporal lobe and the differentiation of the occipital pole (see Fig. 120) give the impression that there has been an actual rotation downwards of the cerebral vesicle on the Island of Reil. The lower end of the stem of the Sylvian fissure also indents the rhinen-

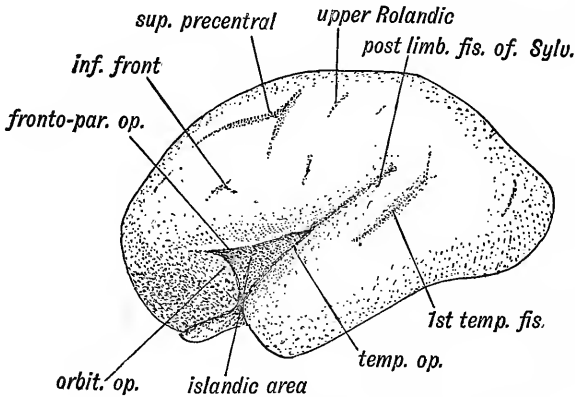


FIG. 121.—The same Aspect during the 7th month.

cephalon, separating the uncinat gyrus from the anterior parts of the rhinencephalon (Figs. 118, 120).

The student is already familiar with the fact that the Island of Reil forms a cortical cap to the corpus striatum. The structures between the islandic cortex and the foramen of Monro represent a section of the thickened wall of the cerebral vesicle (Fig. 109). Convulsions appear on it at the 7th month, when the rest of the cortex also becomes convoluted.

Further, the larger the area of cerebral cortex in any primate, the larger is the Island of Reil; the more convoluted the cortex, the more convoluted the Island. Flechsig has shown that the cortex of the Island is joined to all the cortical areas of the mantle by bands of association fibres. Hence the Island must be regarded as playing a highly important part in co-ordinating the functions of the brain.

The Opercula.—Three opercula grow up and cover the Island of Reil (see Figs. 121 and 122): (1) the temporal, (2) the fronto-parietal, (3) the orbital. The late Professor D. J. Cunningham found that during the

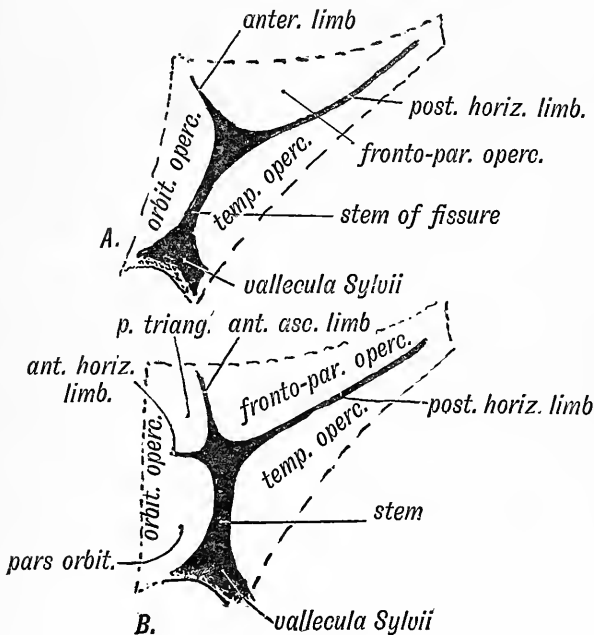


FIG. 122.—Diagram of the Opercula and Fissure of Sylvius.

In *A* the orbital operculum is undivided; in *B* it is subdivided. (After Cunningham.)

later months (7-9) of foetal life an opercular part, known as the **pars triangularis** (Fig. 122, *B*) appeared in quite 50 % of brains and was more frequently present on the left side than on the right, probably owing to the dominant centre for speech being situated on the left side. The pars triangularis is the anterior part of the upper or dorsal operculum (labelled fronto-parietal in Figs. 120, 121), the horizontal limb of the fissure of Sylvius being the anterior continuation of the upper limiting sulcus of the Island of Reil (Elliot Smith). The pars triangularis is cut off from the dorsal operculum by the formation of the ascending limb of the fissure of Sylvius (Fig. 122, *B*). The temporal operculum rises first (5th month), the others a month later. The opercula which bound the posterior horizontal limb of the fissure of Sylvius are the first to come in contact. By the end of the first year after birth all three opercula meet over the Island

and completely hide it. At birth there is still a part of the Island exposed behind the orbital operculum and in lower human races this is frequently the condition throughout life. The anterior opercula (*pars triangularis* and *pars orbitalis*) become part of the centre of speech and represent later additions to the human brain. If the *pars triangularis* be not separated from the dorsal operculum, which is commonly the condition on the right hemisphere, then the anterior limb of the fissure of Sylvius is not subdivided into anterior horizontal and ascending parts (Fig. 122, *A* and *B*). The posterior limb of the fissure of Sylvius is a *limiting* fissure; it separates the audito-sensory area, situated in the first temporal gyrus—especially in the annectant convolutions of this gyrus buried in the posterior part of the Sylvian fissure, from the sensory-motor areas above the fissure.

Comparative Anatomy of the Opercula and Island.—The Island of Reil and its opercula are only well developed in the higher primates. In the typical mammalian brain the upper limiting sulcus of the Island of Reil is represented by the supra-Sylvian fissure (Fig. 125), the inferior limiting sulcus by the pseudo-Sylvian fissure, the anterior limiting by the fronto-orbital fissure (Elliot Smith). There are no opercula—the cortex corresponding to the Island of Reil forms part of the surface of the brain. Figs. 123 and 124, *A*, *B*, represent stages in the evolution of the Island and opercula in the primates. In Fig. 123 the condition in dog-like apes is

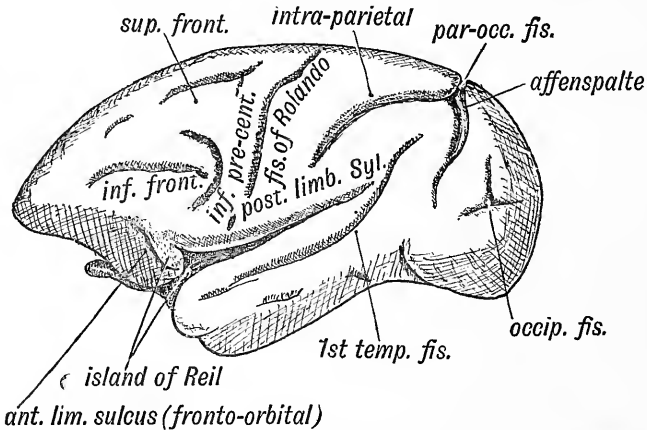


FIG. 123.—The Island of Reil and Fissures on the Lateral Aspect of the Brain of a dog-like Ape.

represented. Only the upper and lower limiting sulci of the Island are hid by opercula, the anterior limiting sulcus (fronto-orbital) being still freely exposed. The Island, which is small, is continuous anteriorly with the frontal lobe. In anthropoids (the gorilla, chimpanzee, orang and gibbon) the Island is larger; the upper and lower limiting sulci are buried; an imperfect anterior limiting sulcus (fronto-orbital fissure) partially separates the Island from the orbital surface of the frontal lobe. In man all three limiting sulci are covered by opercula and completely isolate the Island,

and occasionally this is the condition (Fig. 124, *B*) in the higher anthropoids, but it is in man only that the orbital operculum grows up and meets with the other opercula. This can be the more easily understood when it is remembered that the orbital part of the 3rd frontal convolution is connected with speech.

Hippocampal and Ectorhinal Fissures.—The hippocampal linear depression, which demarcates the hippocampal cortex (Figs. 117, 118) from the neopallial, we have already seen to be a mere superficial indication of a cortical ingrowth (p. 113). The incisura temporalis (Figs. 125 and 118), all that remains of the ectorhinal fissure of the typical mammalian brain, separates the uncus—part of the rhinencephalon—from the cortex

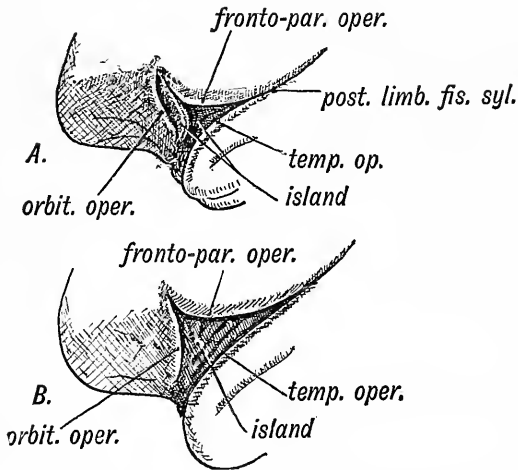


FIG. 124, *A*.—The more common condition of the Island of Reil in Anthropoids.
B.—The complete isolation of the Island of Reil, the condition seen constantly in the Human Brain and occasionally in the Anthropoid.

or neopallium of the temporal lobe. The ectorhinal, or rhinal fissure, as it is usually named, is thus a limiting fissure between olfactory and temporal cortex.

The Calloso-Marginal Fissure.—This fissure on the mesial aspect of the brain arises from the fusion of the genual and intercalary fissures of the typical mammalian brain (Fig. 115). Its origin is probably the result of a pressure due to the growth of the cortex surrounding the corpus callosum, for if that structure be absent, the usual form of this fissure is completely altered. It separates one set of cortical areas from another (Elliot Smith).

The Calcarine and Correlated Fissures.¹—In the typical mammalian brain the calcarine fissure forms part of the same arcuate system as the genual and intercalary (Fig. 115). The part of the cerebral wall in which it is formed projects within the posterior horn of the lateral ventricle (Fig.

¹ See Prof. Elliot Smith, *Journ. Anat. and Physiol.* 1907, vol. 41, p. 198.

226, B, p. 220). The cortex on the lower or posterior lip of the fissure shows the stria of Gennari which characterizes the cortex in which the optic radiations end. The calcarine fissure is thus a limiting fissure formed between striate and non-striate cortex. The **retro-calcarine fissure** or depression, which continues the calcarine sulcus backwards to the occipital pole, is formed by the growth and involution of the striate cortex (Fig. 127). In the ape's brain the striate cortex on the lateral aspect of the occipital pole increases rapidly and rises up as a lip or operculum over the cortex of the parietal lobe. The depression in front of the operculum is known as the **simian fissure** (Affenspalte) or **sulcus lunatus** (Fig. 123). In the human brain the great increase of the parietal cortex, a seat of association centres, has pushed the sulcus lunatus almost to the occipital pole (Fig. 126), or it may, especially in the more civilized races, be

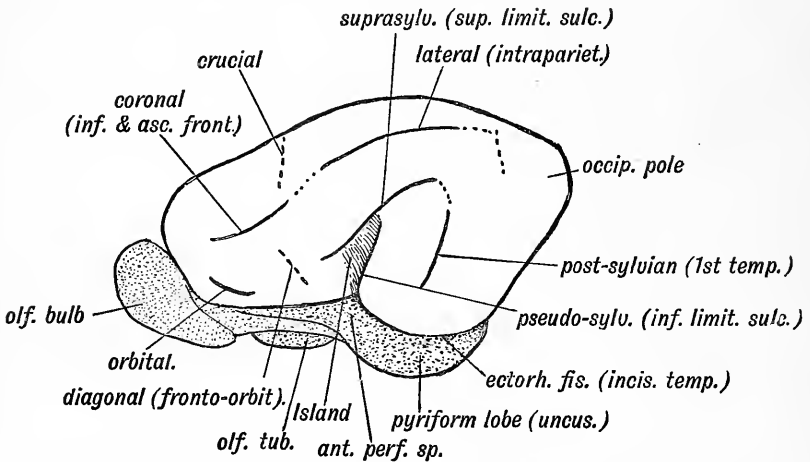


FIG. 125.—The Fissures on the Lateral Aspect of a typical Mammalian Brain. (Elliot Smith.) The Fissures to which these correspond in the Human Brain are indicated within brackets. The parts of the Rhinencephalon are stippled; the cortex corresponding to the Island of Reil, shaded.

completely obliterated. Further the Y-shaped occipital sulcus (external calcarine) on the lateral aspect of the occipital pole (Figs. 123, 126) may join the retro-calcarine sulcus. More recently Elliot Smith has distinguished not only the striate area, in which the optic radiations end, but two surrounding areas, an outer zone—the peristriate, and an intermediate—between the outer zone and the striate area. Certain sulci have arisen in connection with the evolution of these two association or visuo-psychic areas. The **collateral fissure** below the calcarine (Fig. 127) probably results from a mechanical pressure exercised by the growth of the striate area. The **parieto-occipital** fossa or depression on the mesial aspect of the brain results from the inflection of an area of cortex between the calcarine areas of growth behind, and the area of association centres on the mesial aspect of the parietal lobe in front (Fig. 127). The production of the parieto-occipital fossa, with its complex of buried convolutions and sulci, is also related to the growth backwards of the corpus callosum. In human

brains where this structure is absent the buried convolutions and sulci are superficial.

Orbital Fissure.—This fissure is present in most mammalian brains, but its significance is still doubtful.

Fissure of Rolando or Central Fissure, appears during the sixth month as an upper and lower linear depression, which join together in the course of development (Fig. 121). The fissure appears between the motor areas of cortex in front of it, and the sensory areas behind it, and is therefore a limiting fissure. The upper part does not quite correspond to the crucial sulcus of the brain of the cat and dog, for in them that sulcus forms the *anterior* limit of the motor areas (Elliot Smith) (Fig. 125); the lower part may represent part of the coronal fissure. The fissure of Rolando reaches its fullest development in man; it is found only in the higher primates (monkeys and anthropoids).

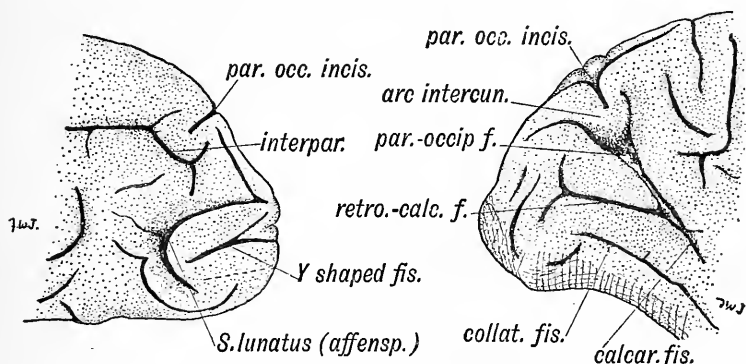


FIG. 126.—The Lateral Aspect of the Occipital Lobe of a Human Brain, showing the Sulcus Lunatus (Affenspalte). (Elliot Smith.)

FIG. 127.—The Mesial Aspect of the Occipital Lobe of a Human Brain, showing the complex nature of the Parieto-Occipital Fissure. (Elliot Smith.)

Sulcus Rectus.—The sulcus rectus, or straight fissure, appears before that of Rolando, and is found in primate brains in which the Rolandic fissure is absent (Figs. 123, 125). It forms in the adult brain (1) part of the inferior frontal fissure, (2) the lower part of the precentral fissure (ascending frontal). It lies between two areas of frontal cortex which are of different structure, and corresponds to the coronal fissure of the cat's brain (Fig. 125).

Intra-parietal Fissure.—The intra-parietal fissure appears between three areas of growth: (1) the cortex of the inferior parietal lobule below, chiefly consisting of association areas related to the visual and auditory and perhaps also to the areas of common sensation; (2) the occipital cortex posteriorly; (3) the cortex behind the upper end of the fissure of Rolando above and in front. It corresponds to the lateral fissure of the cat's brain (Fig. 125), while the whole of the intra-parietal fissure of the ape's brain (Fig. 123) may be regarded as equivalent to the ascending rami in the human brain (Jefferson). The ascending, horizontal and occipital

limbs of this fissure arise independently in connection with separate areas. They may or may not become conjoined. All the parts of the fissure are limiting in nature.¹

Parallel or First Temporal Fissure.—The first temporal fissure separates the first temporal gyrus, in which the auditory centres are situated, from the neighbouring cortex (Figs. 123, 125). As the first temporal gyrus rises to form the inferior operculum of the island of Reil, part of it, in the form of a number of gyri which connect it with the island, are buried in the fissure of Sylvius. In these gyri Campbell has located the terminations of the auditory tracts, the superficial part of the first temporal convolution forming association areas for the auditory centre (Fig. 246). The first temporal fissure corresponds to the post-Sylvian fissure of the typical mammalian brain (Fig. 125).

Secondary Sulci and Gyri.—During the eighth and ninth months the remaining sulci and convolutions of the brain are formed. For the greater part these are peculiar to the human brain.

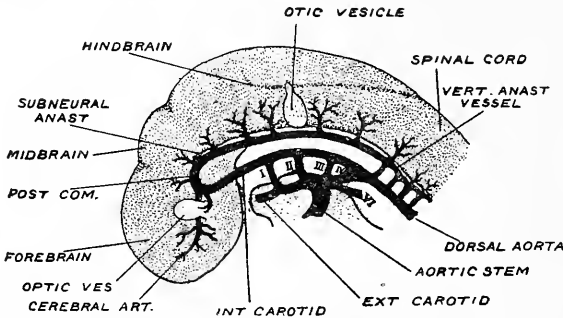


FIG. 128.—Diagrammatic Representation of the Arteries of the Brain at the end of the first month of development. (After Evans.)

Vessels of the Brain.—The embryonic arteries from which the cerebral and vertebral arteries become evolved, are shown in Fig. 128. The dorsal aorta, in which the aortic arches end, is continued forward to the fore-brain, where at the root of the optic vesicle and near the site of the future vallicula of Sylvius it divides into anterior and posterior branches; the anterior branch will become the stem of the middle and anterior cerebral arteries as the cerebral vesicles begin to expand, while the posterior branch becomes continuous with the subneural anastomotic vessel, from which the posterior communicating and basilar arteries will become differentiated and from which the posterior cerebral will arise. The subneural anastomotic chain is fed by segmental vertebral branches of the dorsal aorta (Fig. 128). From this segmental network is formed the vertebral arteries. The right and left anastomotic vessels fuse under the hind-brain during the 6th week to form the basilar artery.²

¹ As to nature of the intra-parietal complex see Geoffrey Jefferson, *Journ. Anat.* 1913, vol. 47, p. 365.

² For further details see Bertha de Vriese, *Archiv de Biol.* 1904, vol. 21, p. 357; F. P. Mall, *Amer. Journ. Anat.* 1905, vol. 4, p. 1; H. M. Evans, *Keibel and Mall's Manual*

The embryological basis out of which the **venous sinuses** and cerebral veins are developed, is shown in Fig. 129. At the middle of the 2nd month the veins of the fore- and mid-brains unite behind the stalk of the optic vesicle to form the *primitive vein of the head*, which passing backwards internal to the Gasserian ganglion leaves the interior of the cranial cavity just in front of the internal ear, passes through in the region of the middle ear to become the jugular or anterior cardinal vein. Before leaving the interior of the skull it receives a cerebellar venous trunk (Fig. 129) and after its exit a medullary trunk—which escapes by the jugular foramen. With the expansion backwards of the cerebral vesicles during the 3rd, 4th and 5th months the system of the longitudinal and transverse sinus becomes evolved by the union of the venous network included in the longitudinal fissure between the cerebral vesicles and between the cerebral vesicles and cerebellum. The main changes are indicated in Fig. 129 ;

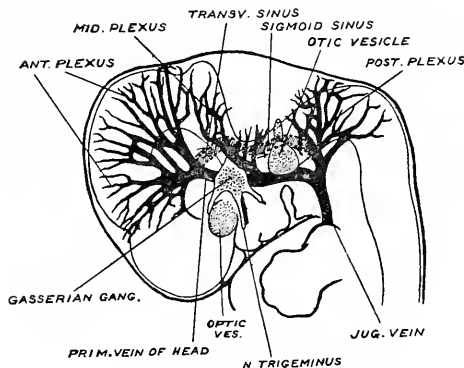


FIG. 129.—The Primitive Vein of the Head and its tributaries in the 6th week of development, with indications of the new anastomotic channels opened up during the 3rd and 4th months. (After Streeter.)

only part of the primitive vein persists—the part lying internal to the Gasserian ganglion which becomes the *cavernous sinus*; the extra-cranial part disappears towards the end of the 2nd month, but it occasionally persists as an emissary vein opening near the root of the zygomatic process. Two important anastomotic channels open up: (1) the precerebellar which drains the tributaries of the fore- and mid-brain into the primitive cerebellar trunk; (2) the post-cerebellar which unites the cerebellar trunk with the veins of the hind-brain; the hind-brain trunk escapes by the jugular foramen. Thus, as the cerebral vesicles grow back their veins are transferred first from the primitive vein to the cerebellar and then to the venous system of the hind-brain. From the anastomotic channel thus opened up are fashioned the transverse and sigmoid sinuses¹ (Fig. 129).

Membranes of the Brain.—Even before the cephalic part of the neural tube is enclosed, mesodermal cells spread in between it and the surrounding
of Human Embryology, 1912, vol. 2, p. 570; G. L. Streeter, *Contributions to Embryology*, 1918, vol. 8, p. 5.

¹ See G. L. Streeter, *Amer. Journ. Anat.* 1915, vol. 18, p. 145; 1916, vol. 19, p. 67.

ectoderm to form a primitive covering. Out of the covering become differentiated the capsule proper of the brain—the *pia-arachnoid* with its vessels, the membranous cranial capsule, from which are differentiated the *dura mater*, enclosing bones and pericranium, and the connective tissues of the scalp. The differentiation of the membranes of the brain and spinal cord is closely related to the establishment of a *cerebro-spinal fluid system*. We have seen that the choroid plexuses of the ventricles of the brain become developed in the 7th week when the human embryo is about 15 mm. long. Dr. L. H. Weed found that at this stage of development in the pig, the cerebro-spinal fluid formed in the 4th ventricle began to escape through a localized area in the inferior medullary velum and to collect in the overlying mesodermal tissue.¹ At the site of escape an opening is formed in the medullary velum, the *foramen of Magendie*, arising in this way. The foramen formed in each lateral recess of the 4th ventricle are produced in a similar manner. The subarachnoid spaces thus commence over the 4th ventricle and round the medulla oblongata and from the region of the hind-brain the system extends proximally and distally until, by the middle of the 3rd month of development, the entire neural tube is enclosed by the arachnoid. The mesodermal condensation which bounds the subarachnoid system becomes the arachnoid; the *pia mater* represents the subarachnoid tissue. At the same time as the subarachnoid spaces are being formed another plane of cleavage sets in external to the arachnoid, the arachnoid being thus separated from the dural layer of the cranial capsule and a potential space produced—the *subdural*. These spaces, particularly the subarachnoid, do not represent parts of the lymphatic system; lymphatic vessels, we shall see, arise like blood vessels; nor does the cerebro-spinal fluid represent a species of lymph.

¹ In connection with the development of the cerebro-spinal fluid system consult: Dr. L. H. Weed, *Anat. Rec.* 1916, vol. 10, p. 475; *Contributions to Embryology*, 1917, vol. 5, p. 3; 1920, vol. 9, p. 425 (production of Hydrocephalus); Percival Bailey, *Journ. Comp. Neur.* 1916, vol. 26, p. 79.

CHAPTER XI.

THE CRANIUM.

Natural Divisions of the Skull.—The human skull is the product of many long epochs, during which it has undergone great changes, but we have every reason for supposing that its general functions have remained much the same since the vertebrate form of animal was evolved. In the first place it has to form a brain-case—a neuro-cranium. Man's brain has reached a degree of development which rendered great changes necessary in this part of the skull. In the second place, the skull has to shelter and protect the special organs of sense—the ear (temporal bone), the eyes (orbits), the olfactory area (nasal region), and taste (bucco-pharyngeal region). In the third place, the skull forms an essential part of the structures concerned in mastication; the facial part of the skull is in reality a scaffolding for the palate and teeth. In the main the facial part of the skull is visceral or splanchnic in function, and hence is sometimes spoken of as the splanchno-cranium. The outstanding characters of the human skull are the great size of the neuro-cranium and the small size of the splanchno-cranium.

Certain Phases in the Evolution of the Skull.—The skull has also been closely related to the function of respiration. In fishes the visceral skeleton of the skull forms the arches which carry the gills. We have seen that the representatives of these arches make a temporary appearance in the head of the human embryo. When a pulmonary replaced a branchial system a nasal airway was separated from the mouth by the formation of a primitive palate, such a palate as is seen in amphibians, reptiles and birds. With the evolution of chewing teeth in the mammalian stock the complete palate was formed, thus allowing the mammalian young to suck, and the adult to chew and breathe freely at the same time. We see all of these stages manifested in the development of the human skull.¹

¹ For recent research on development of skull see: Ed. Fawcett (Chondrocranium of water-rat), *Journ. Anat.* 1917, vol. 51, p. 309; (Chondrocranium of hedgehog), *Journ. Anat.* 1918, vol. 52, p. 211; (Chondrocranium of seal), *Journ. Anat.* 1918, vol. 52, p. 412; (Skull of *Miniopterus*), *Journ. Anat.* 1919, vol. 53, p. 315; C. R. Bardeen, *Keibel and Mall's Textbook of Embryology*, vol. 1, 1910; Warren H. Lewis, *Contrib. Embryology*, 1920, vol. 9, p. 299; John Kernan (Chondrocranium of 20 mm. embryo), *Amer. Journ. Anat.* 1916, vol. 17, p. 605; Chas. C. Macklin (Cranium of 40 mm. foetus), *Amer. Journ. Anat.* 1914, vol. 16, p. 317; R. J. Terry (Chondrocranium of cat), *Journ. Morph.* 1917, vol. 29, p. 281; Eliz. A. Fraser (*Trichosurus*), *Proc. Zool. Soc. Lond.* 1915, p. 299; Philippa C. Esdaile (Chondrocranium of *perameles*), *Phil. Trans. (B)* 1916, vol. 207, p. 439; D. M. S. Watson (*Duckbill*), *Phil. Trans. (B)* 1916, vol. 207,

Cartilaginous Skull.—In trying to interpret the meaning of many of the developmental processes which we see taking place in the human embryo, it is often profitable to seek light from comparative anatomy, and no group of the lower vertebrates can help us in this respect so well as the selachians—the group of cartilaginous fishes to which sharks, rays and dog-fish belong. This is particularly true of the *chondrocranium*—the cartilaginous skull, seen in the human foetus during the 2nd month of development. In Fig. 130 is represented the cartilaginous cranial wall which encloses the brain of a shark; we see at once that the base is made up of two parts—a *chordal* in which the remains of the anterior part of the notochord are embedded and a *prechordal* lying in front of the notochordal part. The fossa for the pituitary body occupies the posterior part of the prechordal base. The chordal part represents a continuation forwards of the vertebral column, only the cartilage never becomes segmented but remains as a continuous plate, and thus gives solidity to the part. Signs of segmentation are seen in the series of foramina by which the roots of the

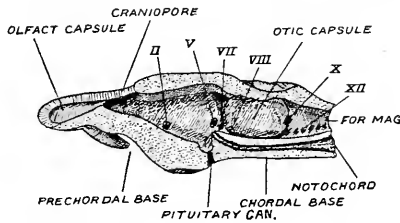


FIG. 130.—The Chondrocranium of a Shark laid open by a mesial sagittal section. (After Gegenbaur.)

hypoglossal nerve escape. The supra-chordal part of the cranial cavity is occupied by the hind- and mid-brains, which also show traces of a segmental origin. In the lateral wall of this part of the skull is also placed the otic vesicle—the vestibular or balancing apparatus. It will be remembered that it was the attachment of this organ to the hind-brain which occasioned the development of the cerebellum; it also gives rise to a disturbance of the skull, for the cartilaginous capsule which is developed round the otic vesicle is thrust into the cranial wall and pushes backwards the representatives of the neural arches of the chordal cranium (Fig. 130).

The prechordal part of the skull serves as the capsule of the fore-brain. At no time is there a segmentation of the fore-brain or of its cranial capsule; we are here dealing with a part of the skull which lies in front of the ancient vertebral region, and has arisen, as has the fore-brain itself, in connection with two organs of sense—the nose and eye. The olfactory organ is enclosed in a capsule of cartilage which is placed like the watchman of a ship, on the prow of the primitive skull of all aquatic vertebrates. The capsule of the otic vesicle never forms part of the cranial wall, but becomes differentiated to form the sheath of the optic nerve and of the eyeball.

p. 311; (Amphibia), *Phil. Trans.* (B) 1919, vol. 209, p. 1; E. S. Goodrich (Cranium of dog-fish), *Quart. Journ. Mic. Sc.* 1918, vol. 63, p. 1; Graham Kerr, *Textbook of Embryology*, vol. 2, 1919.

If we examine the chondrocranium of a human foetus in the 8th week of development (Fig. 131) we note the same divisions as are shown in Fig. 130. The base shows chordal and prechordal parts. In the chordal part we note the cartilaginous otic capsule thrusting backwards the combined occipital elements in the lateral wall; we see the prechordal part passing forwards as a rostral beam to support the nasal or ethmoidal capsule. But of the cartilaginous roof only mere remnants are present. There is: (1) the *tectal plate*, or parietal plate as it is sometimes named; it is attached, along the lower border, to the auditory capsule and occipital element; (2) there are two small processes springing from the sides of the prechordal base (Figs. 131, 132)—the *ala temporalis*—the fundament from which the great wing of the sphenoid will be developed and the *orbito-sphenoid*—the plate from which the small wing will be fashioned. These three carti-

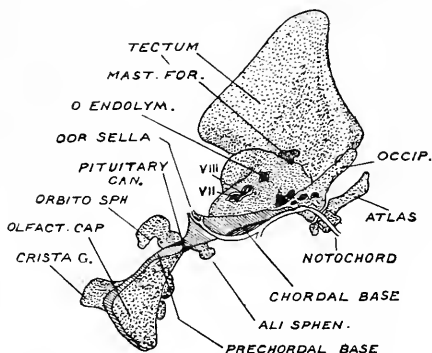


FIG. 131.—Sagittal Mesial Section of the Chondrocranium of a Human Foetus 20 mm. long and in the 8th week of development. (Warren Lewis.)

laginous plates are all that appear in the human embryo to represent the cartilaginous roof of the primitive skull.

If we turn to Fig. 132 we can see why the primitive cartilaginous skull of the human embryo has become so profoundly modified and reduced. It is a result of the large mass attained by the mammalian central nervous system at an early state of development. When a builder is to erect a great edifice he does not begin by repeating the evolutionary history of house building, but marks out from the beginning the extent of his foundations. It is so in laying down the human brain; it is laid down on big lines almost from the first; the ancient roof has become altogether inadequate; we see the tectal plate growing up and covering the roof of the 4th ventricle; it meets with its fellow of the opposite side and forms that part of the occipital bone which completes the posterior fossa of the skull and encloses the hind-brain. But all the rest of the roof is formed by a membranous capsule in which cartilage never develops. A glance at Fig. 132 will show why the roof must be fashioned from plastic material, for during the 3rd, 4th and 5th months the cerebral vesicles, lying over the prechordal region of the base, expand upwards and backwards until their occipital poles reach the tectal plates.

There are certain other features seen in the lateral aspect of the foetal chondrocranium which call for comment here. The auditory capsule, the auditory ossicles and the region of the tympanum, save for their covering of soft parts, lie exposed on the surface of the skull. If we turn to the lateral

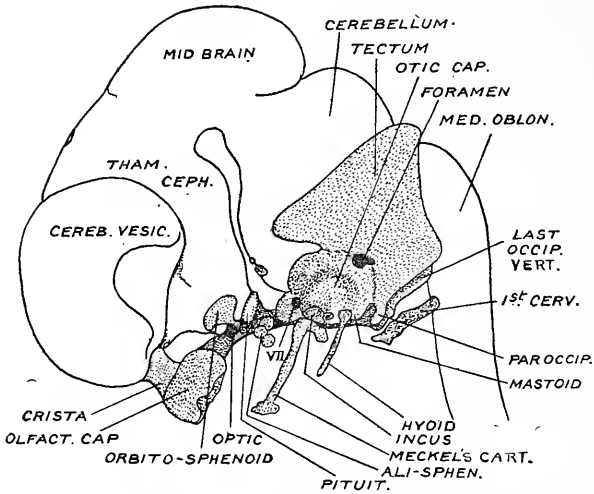


FIG. 132.—Chondrocranium of a Human Embryo in the 8th week of development, seen from the side. (Warren Lewis.)

aspect of the cartilaginous skull of a shark we obtain an evolutionary explanation of this arrangement. At the anterior end (Fig. 133) is seen the nasal or ethmoidal region; the hind end is formed by the occipital area—compounded from occipital vertebrae. Between these two extreme areas lies a large intermediate part which is definitely demarcated into

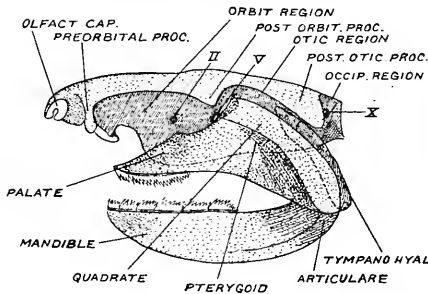


FIG. 133.—Lateral Aspect of Skull of Shark. (After Gegenbaur.)

two regions—orbital and otic (Fig. 133). Lying on the otic area and attached to it are the primitive maxillary apparatus—the tympano-hyal (Fig. 133) which corresponds to the stapes, the quadrate part of the palato-quadrate—which has been shaped in mammals to form the incus, and the upper end of the primitive mandible which gives rise to the malleus—all

lying exposed just as in the human embryo. The cartilaginous prominence—named post-orbital in Fig. 133, because it bounds posteriorly the orbital region of the primitive skull—is worthy of note because it represents the point at which a new mandibular joint—the *temporo-mandibular*—becomes evolved in mammals, and thus sets free the old maxillary parts for the service of the ear. The post-orbital process of the primitive skull becomes the site of the articular eminence in the mammalian skull, while the pre-orbital is represented by the internal angular process of the mammalian orbit. Thus, out of the primitive orbital region is fashioned, not only the orbit, but the whole floor of the temporal fossa, the malar bone and zygomatic arch being later formations evolved out of membranous skeletal elements. Similarly in the skull of the human embryo, as in that of the shark, there are no cartilaginous representatives of the maxilla or premaxilla.

Growth of the Cranial Cavity.—The neuro-cranium is framed by the disposition of its bones and sutures, so as to allow a free and easy expansion of the brain. By a mechanism we do not fully understand the bones entering into the formation of the cranial cavity grow as demand is made on them by the brain; at least, this is so in early life. When the cranial bones begin to form in the latter part of the second month, the brain (cerebral vesicles) is only half an inch long—from frontal to occipital pole; in the adult the length is fourteen times as much and its volume fifteen hundred times larger. As the cerebral vesicles expand the developing bones alter in shape. By the 7th month of the foetal life the relative proportions become approximately fixed. During the first four years of life, brain and cranial growth go on rapidly. At birth the brain has attained from 20 to 22 per cent. of its size; by the 4th year over 80 per cent. of the volume is already present. There is a steady increase until the 18th or 20th year, when the maximum is obtained (about 1500 cubic centimetres in Englishmen); after then there is a decline in the capacity of the cranium. The changes in the cranial walls are secondary to those in the brain.

From Fig. 134 it will be apparent that the walls of the cranium are made up of two very different parts—basilar and capsular. The basilar part is thick and developed in a cartilaginous basis. Growth proceeds as in a long bone; the lines between the basi-occipital and basi-sphenoid, the basi- and pre-sphenoid, and between the pre-sphenoid and ethmoid are growth or epiphyseal lines. The growth of the base of the skull is determined as much by the needs of the splanchno-cranium as by those of the neuro-cranium. The capsular part—occipital, parietal, frontal and temporal bones—on the other hand, respond easily to the expansion of the brain. They grow at their edges; the sutures are growth lines. Growth at the coronal and lambdoid sutures adds to the calvarial length; growth at the sagittal and squamous sutures increases the calvarial breadth. At the same time there is also a constant deposition or growth on the outer table and an absorption on the inner. In this manner the bones are modelled, and growth of cranial cavity and brain are co-ordinated. Only those bones which enter into the formation of the cranial cavity and help to form the brain chamber are dealt with in this chapter. These bones are the frontal, parietal, occipital, temporal, ethmoid and sphenoid.

Is the Skull made up of Segments?—We have just seen that the body is made up of 33 or more segments. Is the skull made up of a series of segments? The theory supported by Owen and many others that the cranium is really composed of four modified vertebrae is now no longer tenable. On the other hand the arrangement of the nerves and muscles, the evidence of development and comparative anatomy, indicate that it is composed of a number of segments, probably nine in number. The four posterior, which form the occipital region of the skull, are recognizable at

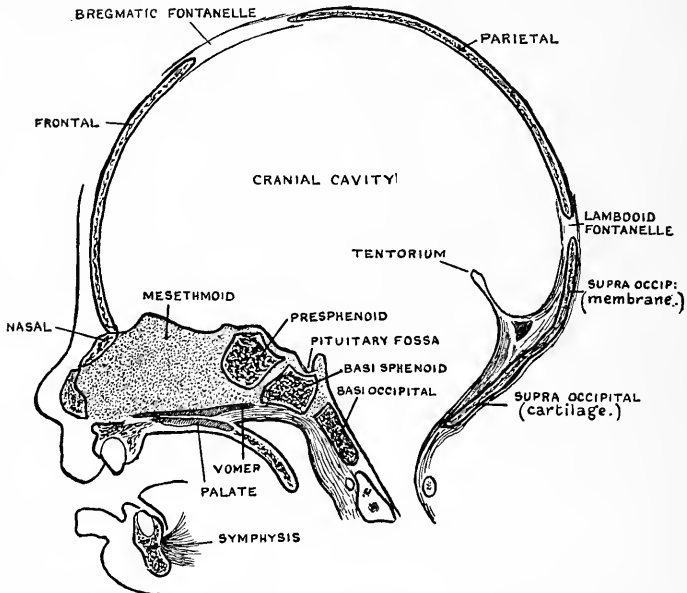


FIG. 134.—Median Sagittal Section of the Skull of a Foetus of the ninth month.

an early stage of development, but at no period in the development of the embryo has cranial segmentation been seen anterior to the otic vesicle.

The Primitive Membranous Skull.—The brain is developed in the same manner as the spinal cord from the medullary plates of the neural groove. In the same manner the mesoderm grows under and over the cephalic part of the neural canal, and forms for it a **mesenchymal** or membranous covering. The covering of mesoderm thus formed is the primitive *Anlage* of the skull in the embryo.

Membrane and Cartilage Bones.—Only the base of the human skull is developed in cartilage, the rest is developed in membrane. How has such a condition arisen? The brain of amphioxus, if it can be said to possess one, is wrapped in a membranous covering. In fishes with cartilaginous skeletons this embryonic mesodermal capsule becomes chondrified—plates of cartilage develop in it. As in the spinal column, the process of chondrification begins at the base and spreads slowly round to the crown or dorsum of the head. The cartilaginous cranium is an advance on the

membranous stage. In many fishes a further most important element is added. The **dermal** bony plates, to which the placoid scales are fixed, are applied to the cartilage over the sides and dorsum of the skull. Thus to the cartilaginous element of the skull is added a third element—bone formed in membrane. Now, in the mammalian skull, and especially in that of man, the cerebral vesicles grow so quickly that long before the process of chondrification has had time to spread in the membranous capsule from the base to the crown, the dermal bones have formed, and thus supplant the cartilage on the calvarium. Hence, in the human skull, while the process of chondrification occurs in the base, and afterwards undergoes ossification, the roof and sides (calvaria) of the skull are formed by bones which, historically, are **dermal bones**, and hence are formed directly

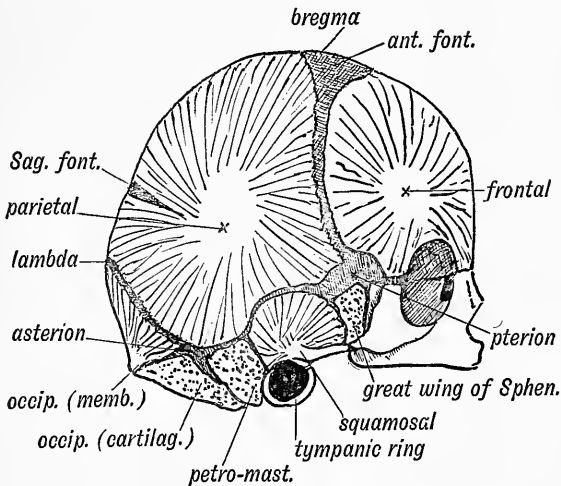


FIG. 135.—The Centres of Ossification for the Dermal Bones of the Skull. The bones which are formed in cartilage are stippled.

in membrane. The dermal bones of the human skull are : (1) the frontal, (2) the parietal, (3) the inter-parietal part of the occipital (the part above the superior curved lines), (4) the squamous part of the temporal.

Thus the calvarial part of the skull passes directly from the membranous to the bony stage, while the base of the skull, like the spinal column, passes through three stages : (1) membranous, (2) cartilaginous, (3) bony. It will be thus seen that the base of the skull, developed in cartilage, is the most ancient part, while the dermal bones, which form the calvaria, represent a later addition.

Development of the Calvarial (membranous or dermal part) of the Skull.—In the 8th week of foetal life—the foetus being then about 25 mm. (1 in.) long—there appear on each side of the membranous cranial capsule four centres of ossification :

(1) For the frontal bone, at a point which becomes afterwards the frontal eminence (Fig. 135) ;

(2) For the parietal, at the position of the parietal eminence ; this

centre is double or even triple in nature, but the separate points are placed closely and soon fuse together ;

(3) For the squamosal, at the base of the zygoma (Fig. 135) ;

(4) For the membranous part of supra-occipital (part above superior curved line). Maggi and Hepburn¹ have shown that there may be four centres (two on each side) in the membranous supra-occipital (Fig. 137).

The two or four occipital centres fuse early into one at the position of the external occipital protuberance, but occasionally these centres may form two, three or four separate bones. The two frontal ossifications fuse about the end of the first year ; the **metopic** suture,² which separates them, disappearing then. This suture occasionally persists. One or both parietals may be divided by a suture or by a complex of sutures.³ The

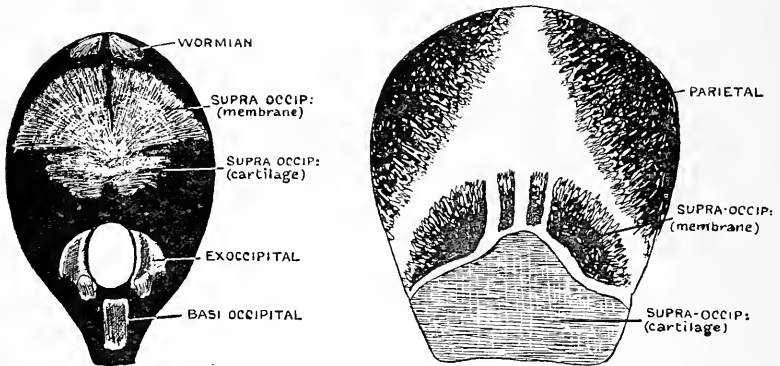


FIG. 136.—The Occipital Bone at the 4th month, showing pre-interparietal Wormian Bones. (After Sappey.)

FIG. 137.—The Supra-occipital from a Foetus of 3 months, showing four Centres of Ossification for the Membranous Supra-occipital. (After Maggi.)

centres of ossification in these cases have not fused. The parietal bones ossify together, at the sagittal suture, late in life, commonly between the 35th and 45th year, when the growth of the skull has entered a retrograde phase. The squamosal partly covers the petro-mastoid cartilaginous element and fuses with it in the first year, the temporal bone being thus formed. These bones, as they are laid down, accurately follow the contour of the brain. That organ forms a relatively small sphere when ossification commences. Hence the convexities or **eminences** at the regions of earliest formation.

The Manner in which these Bones are Developed.—In Fig. 138 a vertical section of the skull of a foetus 5 months old is represented. The coverings of the brain are seen to be then (1) scalp, (2) a stout white fibrous capsule, (3) a fine membrane lining it—the inner layer of the dura mater, (4) the arachnoid covering the brain (not shown in figure). Ossifying

¹ Professor D. Hepburn, *Journ. Anat. and Physiol.* 1907, vol. 42, p. 88.

² Professor T. H. Bryce, *Journ. Anat.* 1917, vol. 51, p. 153; Dr. A. H. Schultz, *Amer. Journ. Anat.* 1918, vol. 23, p. 259.

³ Professor Patten, *Zeitschrift für Morph. und Anthrop.* 1912, vol. 14, p. 527; Professor R. J. A. Berry, *Journ. Anat. and Physiol.* 1910, vol. 44, p. 73.

fibres which form the parietal are seen developing within the capsule and radiating out from the centre of ossification. The ossific fibres, as they spread outwards from a common centre, unite by branches, thus forming an irregular network with osteoblasts and growing vessels within its meshes. Lower down are seen the ossifying fibres of the squamosal. The base of the skull is formed of cartilage which is covered, or ensheathed, by a perichondrium continuous with the membranous capsule. In the cartilage appear the centres of ossification for the sphenoid.

As the bony fibres of the parietal spread out, they divide the primitive cranial capsule into an outer layer—the **pericranium**—and an inner—the **periosteal** layer of the dura mater. At the periphery of the bone and in the sutures the continuity of these two layers persists. The growth of the fibroblasts and osteoblasts in the sutural lines between the bones keeps

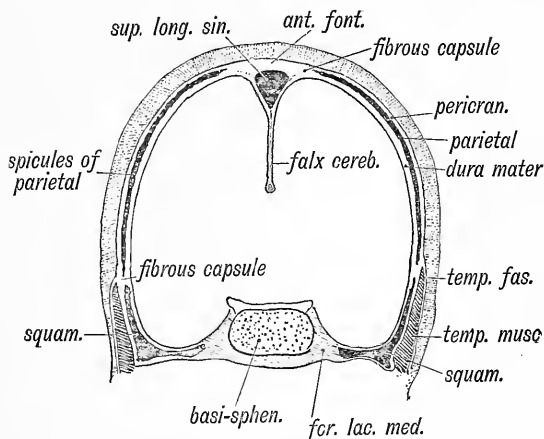


FIG. 138.—A Coronal Section of the Skull of a Foetus, 5 months old.

time with the growing brain which expands the capsule, but there is, at each corner of the parietal bone, until the end of the first year, a part of the primitive cranial capsule left unossified. These unossified parts of the membranous capsule are the **fontanelles**.

The Fontanelles.—There are five fontanelles connected with each parietal bone, one at each of its rounded angles, and one, the **sagittal** (Fig. 135), which occurs between the radiating fibres of the parietal near the posterior end of the sagittal suture. The parietal foramen marks its position in the adult. In about 15 % of children this fontanelle is un-closed at birth; a large parietal foramen may permanently mark its situation. The posterior inferior fontanelle, situated at the **asterion** (Fig. 135), the anterior inferior at the **pterion**, and the posterior superior at the **lambda**, close before or about the time of birth. Separate ossifications, which become **Wormian** bones, are often developed in the primitive capsule of the skull at those three fontanelles and thus close them. The anterior superior fontanelle, at the **bregma**, cannot be distinctly felt during life after the first year (Warner), but it is not completely closed until the second

year is nearly over. This fontanelle is lozenge-shaped, being bounded by four bones, viz. the two parietals and two frontals. The bregmatic or anterior superior and lambdoid or posterior superior fontanelles are median and common to both parietals.

The membrane-formed bones consist at first of a thin lamella of osseous fibres radiating out from the point at which ossification commenced. The osteoblasts beneath the pericranium on the outer surface of the lamella and the dura mater on the inner surface, deposit bone, and by the 5th year an outer and an inner table, with diploic tissue between, are developed. Into the diploë of the frontal bone protrude the growing buds of the two frontal sinuses. As the brain expands new bone is formed at the sutures to increase the capacity of the skull, but the operation of craniotomy to allow the expansion of a confined brain, by the formation of a new suture, is founded on the assumption that the arrest of brain-growth in microcephalic idiots is due to the closure of the sutures, whereas it is probably due to an inherent defect in the growth of the brain. We frequently see skulls where one or more sutures have been prematurely closed, but in such cases there has been compensatory growth at other sutures, giving rise to a peculiarity in cranial form. Growth of the cranial cavity could take place by a deposit of bone on the outer table and an absorption from the inner; for this manner of growth, sutures are unnecessary. The synostosis of the sutures does not necessarily prevent growth; synostosis of the skull bones occurs only when the brain has ceased to expand. If the brain of the infant is arrested in its growth, premature ossification of the sutures occurs, the condition of **microcephaly** resulting therefrom. In **hydrocephaly**, when the ventricles become enormously dilated, the membranous capsule of the cranium expands so quickly that the process of ossification cannot keep up with its rapid growth. Hence in hydrocephaly the fontanelles are enormous. The growing points of ossific fibres are detached and form Wormian bones. The cartilaginous part of the skull is scarcely affected in this disease. The membrane-formed part of the skull is liable to diseases which do not affect the cartilage-formed part. The dura mater is very adherent to the bones formed in cartilage.

Development of Bones formed in Cartilage.—(1) **The Occipital Bone.**—The occipital bone is developed from the **parachordal cartilages**. Two cartilaginous bars, although appearing separately in the development of fishes, are united from their first appearance in the human embryo, forming a **basilar plate** (Robinson). The plate is formed in the mesenchymal sheath of the notochord, its centre of chondrification—the first in the base of the skull—appearing at the end of the 1st month of development. The basal plate may be regarded as a continuation of the vertebral bodies, while the lateral processes (Fig. 140) which are perforated at their bases by the foramen or foramina for the hypoglossal nerve and which separate the jugular foramen in front from the foramen magnum behind, may be regarded as a continuation of the neural arch series.¹ Fused to the lateral

¹ For the variations in the manifestation of partly separated occipital vertebrae see Gladstone and Powell, *Journ. Anat.* 1915, vol. 49, p. 190; Elliot Smith, *Brit. Med. Journ.* 1908, II. p. 594. See also references p. 56.

process and also to the otic capsule is the roof plate already mentioned—the **tectal plate** (Fig. 132). While the lateral processes never reach the posterior or dorsal margin of the foramen magnum, it is quite otherwise with the right and left tectal plates; they extend round the hind-brain until they meet and unite, thus forming the posterior margin of the foramen magnum and the supra-occipital plate of cartilage. Thus the cartilaginous basis of the occipital bone is formed out of three elements on each side—the basal plate representing the centre and hypochordal arches of cervical vertebrae, the lateral processes, corresponding to the neural vertebral arches and an extra element—the tectal plate.

In Fig. 140 the condition of the occipital region is shown in a 5th-month foetus. Four centres of ossification appear in the tectum (Fig. 137), and quickly fuse to form the cartilaginous part of the supra-occipital. A

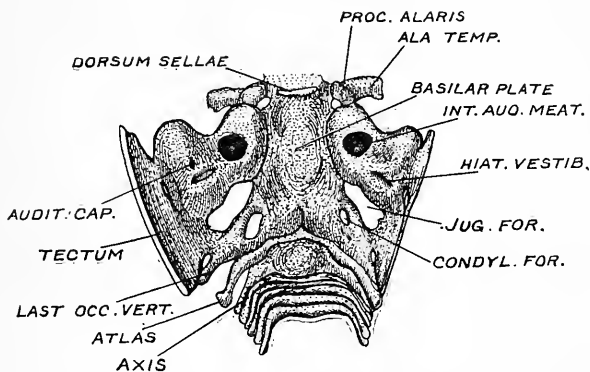


FIG. 139.—Cranial Aspect of the Basal Plate and Occipital Parts of the Chondrocranium of a Human Foetus in the 8th week of development. (Warren Lewis.)

suture between the membranous and cartilaginous parts is clearly visible—especially near the fontanelle at the asterion. The membranous and cartilaginous parts of the supra-occipital become completely fused soon after birth. It will be observed that the process of fusion between the lateral parts of the cartilaginous supra-occipital is not complete in the 5th month (Fig. 140). The occipital fontanelle projects upwards between them from the foramen magnum. This fontanelle is filled by a continuation of the posterior atlanto-occipital ligament, and becomes closed soon after birth. It is the most common site of a cerebral meningocele—a sacular protrusion of the membranes of the brain which contains cerebro-spinal fluid, and usually a part of the occipital lobes distended by a dilatation of the posterior horns of the lateral ventricles.

Separate centres of ossification appear in the occipital cartilages to form (1) the basi-occipital, (2) the two exoccipitals, and (3) the supra-occipital.¹ The occipital consists of four pieces until the fourth year, when synostosis occurs. The occipital condyles are formed from the exoccipitals and

¹ For a very complete account of the dates at which all centres of ossification appear in the skeleton see Mall, *Amer. Journ. of Anat.* 1906, vol. 5, p. 433.

basi-occipital, the exoccipital element constituting in the adult by far the larger part, but when the condyles first appear they are continuous at the anterior border of the foramen magnum, forming a single or median condyle as in reptiles, birds, and lower mammals. The foramen for the hypoglossal nerve, which may be subdivided into two or even three compartments, is formed between the two elements and thus corresponds to the inter-vertebral series. The occipital protuberance is formed by both membranous and cartilaginous parts of the supra-occipital.

(2) **The Petro-mastoid** forms part of the base of the skull. We shall see that the petrous bone (p. 224) is primarily developed as an independent cartilaginous capsule round the inner ear, but at an early date (6th week) it fuses at certain points with the parachordal basis of the occipital bone,

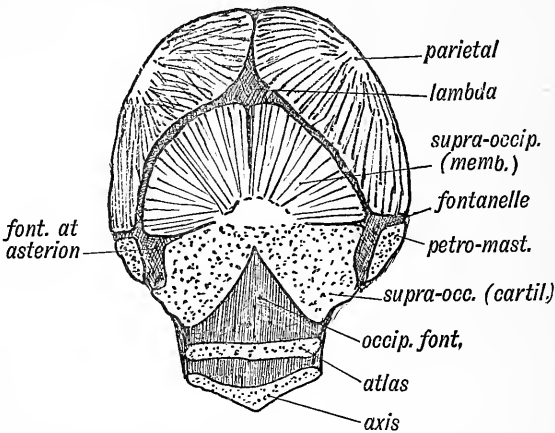


FIG. 140.—The Occipital Region, in a Foetus of 5 months.

while an extension from the mastoid part of the capsule enters into the formation of the tectum. Even as late as the thirtieth year remnants of the tectal cartilage may be found between the petro-mastoid and occipital bones, especially between the jugular process of the occipital and the mastoid. The fibro-cartilage in the foramen lacerum medium and perhaps Eustachian cartilage, which is continuous with it, are remnants of the periotic cartilaginous capsule.

(3) **Trabeculae Cranii.**—The basilar plate, containing the notochord and fashioned out of the parachordal cartilages terminates in the dorsum sellae, in the hind wall of the pituitary fossa. The prechordal part of the base of the skull, in the lowest vertebrates, appears first as two irregular plates of cartilage—the trabeculae cranii (Fig. 141). Even in the mammalian skull the trabeculae can still be traced in the pituitary region (Fawcett). Their posterior extremities fuse round the anterior termination of the notochord with the basilar plate. The buccal part of the pituitary grows into the cranial cavity in front of the notochord and keeps the two cartilages apart; but in front of the pituitary the two bars fuse in the

middle line. The mesial fused parts of the trabeculae grow into the embryological basis of the nasal septum (Fig. 142). The posterior part of the median fused bars forms the cartilaginous basis of the pre-sphenoid and basi-sphenoid (Fig. 142).

Development of the Sphenoid.—

Recently Professor Fawcett¹ has examined the manner in which the cartilaginous basis of the sphenoid is formed in the human embryo. The mesodermal or mesenchymatous basis of the sphenoid becomes chondrified during the second month—right and left centres representing the original trabeculae. While the cartilage, in which the centres for ossification of the basi- and pre-sphenoids appear, is formed out of the trabecular or prechordal plate, the great and small wings have a separate origin. We have already seen (p. 137) that on each side of the prechordal plate there are formed two plates of cartilage,

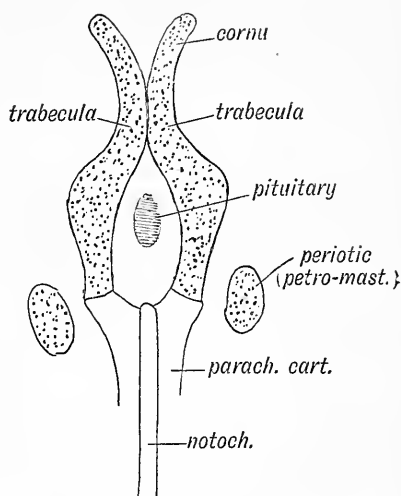


FIG. 141.—Diagram of the Trabeculae Cranii, Parachordal Cartilages, and Periotic Capsules.

rudiments of the lateral wall and roof of the primitive cartilaginous cranium (Fig. 133). The anterior of these—the **orbito-sphenoids**—form the cartilaginous basis of the lesser wings. In the 8th week of development (Fig. 142)

each is a sickle-shaped plate lying over the stalk of the optic vesicle, sending one process under the optic nerve to join the cartilaginous prominence—the *processus hypochiasmata*—from which the muscles of the eyeball take origin. The other process of the orbito-sphenoid fuses with its fellow above the prechordal plate and thus completes the optic foramina (Fig. 143). The great wing or **alisphenoid** arises in a rather complicated manner. In

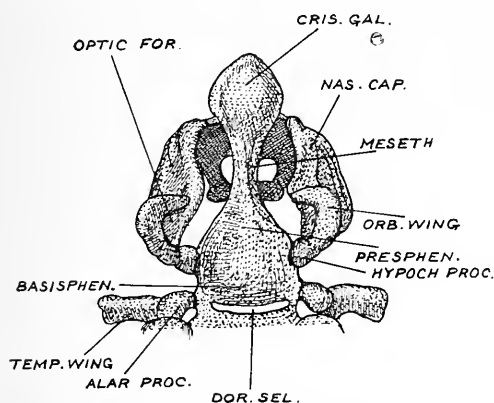


FIG. 142.—The Prechordal Base of the Chondrocranium in the 8th week of development. (Warren Lewis.)

the 8th week it is represented by two small nodular masses of cartilage (Fig. 142), the alar process attached to the prechordal plate and the temporal wing. The internal carotid artery lies on the mesial side of the alar process, which is represented merely by the lingular process of the fully

¹ *Journ. Anat.* 1910, vol. 44, p. 303. See also references, p. 135.

developed bone. The temporal wing lies under the Gasserian ganglion and separates the 2nd from the 3rd division of the nerve. The mesodermal tissues round the temporal wing undergo a secondary chondrification, and it is from this new formation that the greater part of the ali-sphenoid is formed; as it extends it encloses the 2nd and 3rd divisions of the fifth nerve, the round and oval foramina being thus formed. A gap remains between the orbito-sphenoid and ali-sphenoid to form the sphenoidal fissure. The dorsum sellae may have a separate centre of chondrification.

At birth the sphenoid bone consists of three parts, the great wings being separated from the rest of the bone. The **sphenoidal turbinate**

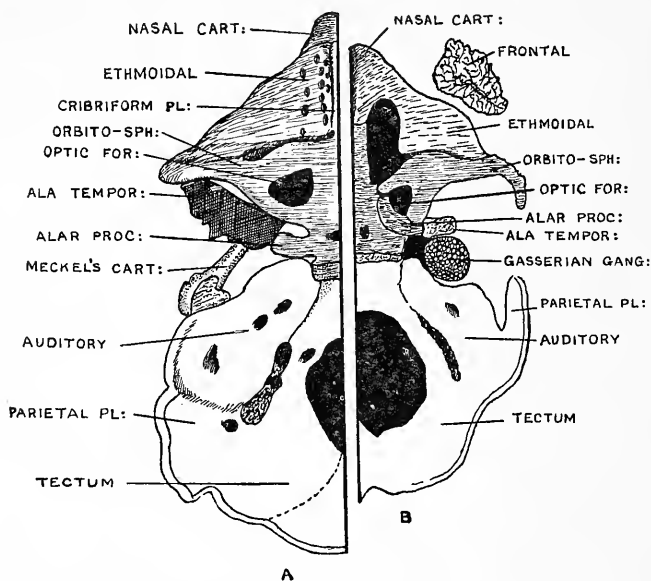


FIG. 143, A.—Left half of the Cartilaginous Basis of the Skull in a Foetus of 3½ months. (After Kollmann.)

B.—Right half of the Cartilaginous Basis of the Skull in a Foetus of 2½ months. (After Fawcett.)

bones, afterwards inflated by the development of the sphenoidal air sinuses, are then nodules of bone, surrounded by cartilage. They also are separate and are derived from the lateral ethmoidal cartilaginous plates which represent the olfactory capsule. The **internal pterygoid** plates are also separate ossifications laid down in the membrane over a plate of cartilage, representing part of the palato-quadrate bar of lower vertebrates (Fig. 133). Only its hamular process is formed in cartilage (Fawcett). The internal becomes adherent to the external plate during the fourth month of foetal life. The external plate is developed as a membranous outgrowth from the ali-sphenoids or great wings. The pre-sphenoid unites with the basi-sphenoid in the 8th month; the great wings unite with the basi-sphenoid soon after birth. The **lingula** (alar proc. Fig. 143, B) which bounds the outer side of carotid groove is ossified from a centre which appears during the 4th month of foetal life.

The wings of the sphenoid develop in the orbital region of the primitive skull (Fig. 133). The enormous expansion of the cerebral vesicles and the evolution of a new system of mastication have worked a revolution in the primitive orbital region; the temporal lobes, as it were, have burst the ancient cartilaginous wall. The ala-temporalis appears first in the embryo as a process from which the muscles of mastication take origin (Fawcett).

The Pituitary Body is developed between the trabeculae cranii; the pre-sphenoid is formed in front of it and the basi-sphenoid behind it. A canal may remain in the foetal or even adult bone to mark the point of ingress of the buccal part of the pituitary.¹ The wings of the vomer cover the opening of the pituitary canal on the pharyngeal aspect of the skull, if it be present. On the cerebral aspect it opens at the olivary eminence which also marks the union of the pre- and the basi-sphenoids. The writer has seen a child, in which the trabecular cartilages had remained

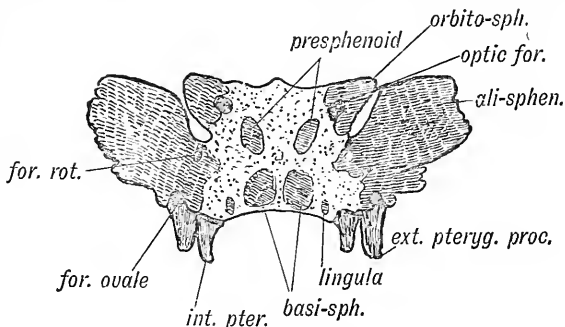


FIG. 144.—The Sphenoid in a Foetus of 4 months. The Centres of Ossification are deeply shaded. (After Sappey.)

apart, leaving a wide gap through which the pituitary projected within the septum of the nose. The pre-sphenoid and afterwards the basi-sphenoid are much altered by the growth of the sphenoidal sinuses which commence to expand rapidly about the 7th year.² The great wings support the temporal poles of the brain, their size depending on the development of that part of the brain. They are much larger in man than in any other mammal, owing to the great size of the human temporal lobes. The small wings project within the vallecule Sylvii. In the early foetus the dorsum sellae is enormously developed, and fills the deep and sharp angle between the mid-brain and fore-brain (Fig. 85).

The Ethmoid.—The cartilaginous basis of the skull is completed in front by the ethmoid; on its upper surface rest the olfactory bulbs. In the primitive skull (Figs. 130, 133) the olfactory capsule, out of which the cartilaginous ethmoid has been evolved, is far in front of the space which contains the fore-brain. It has been brought within the floor of the cranial cavity by a double process—by a shortening of that part of the trabecular plate which unites the sphenoid to the olfactory or ethmoidal capsule, and by the forward extension of the cerebral vesicles which have

¹ H. Wrai, *Anat. Hefte*, 1907, vol. 33, p. 411 (Cranio-pharyngeal Canal).

² V. Z. Cope, "Ossific. of Sphenoid," *Journ. Anat.* 1917, vol. 51, p. 127.

pushed their way into the forehead until they project beyond the olfactory region. The cribriform plate is formed in the 4th month; up till then a gap separates the lateral mass from the septal or trabecular plate (Fig. 143).

Formation of Foramina in Bone.—The foramina of the skull are formed in one of three ways (Bland-Sutton):

(1) By the union of two bones; examples of this form are the jugular foramen, sphenoidal fissure, Glaserian fissure, etc.

(2) By the union of two elements of one bone; the anterior condyloid foramina, optic foramina, the foramen magnum, aqueductus Fallopii, etc.

(3) By the enclosure of a notch on the edge of a bone of which the foramen ovale is the best example. This foramen is at first a notch in the posterior border of the great wing of the sphenoid (Fig. 144); it remains in this condition in all mammals except man. In him the margins of the bone on each side grow out and fuse, and thus convert the notch into a foramen. Other examples are the foramen spinosum, the foramen rotundum, parietal foramen, mastoid, etc.

Wormian Bones.—In the six fontanelles which occur at the parietal angles ossific centres frequently appear. Fontanelle ossifications form Wormian bones. They occur most frequently at the posterior angles of the parietal (Λ and Asterion); they are also common at the Pterion (epipteric Wormian) but rare at the Bregma. The Wormian at the last-mentioned point receives the name of *os anti-epilepticum*. Much confusion has been caused by naming a large Wormian, which may occur in the lambdoidal (posterior-superior) fontanelle, the inter-parietal bone. Wormian or sutural bones are particularly numerous in the skulls of infants who have been the subjects of hydrocephaly. It is possible that, during the rapid expansion of the skull, the tips of ossifying fibres become detached, thus forming separate centres of ossification in the sutures and fontanelles.

The Inter-parietal Bone.—It has already been shown that the part of the supra-occipital above the superior curved lines is developed from membrane by four centres of ossification, and is at first, and almost until birth, nearly separated from the lower part developed from cartilage (Figs. 137, 140). The membranous part of the supra-occipital represents the inter-parietal bone. In marsupials, ruminants and ungulates, the inter-parietals fuse with the parietals, and not with the occipital. In rodents they fuse with both occipitals and parietals. In primates and carnivora, as in man, they fuse with the occipital. It is extremely rare to find the whole inter-parietal as a separate bone in man, but a large Wormian, partly replacing the inter-parietal, is very frequent. Such a Wormian bone, if large, is named variously, *os epactal*, *os Incae*, *os triquetrum*, or *pre-interparietal*.

The Post-frontal does not occur in mammals as a separate bone; in them it has fused with the frontal, and forms that part of the bone which articulates with the great wing of the sphenoid and malar. A Wormian bone—the epipteric—which is occasionally developed in the fontanelle at the pterion, may be mistaken for it. Traces of a true post-frontal, partly separated from the frontal, rarely occur in man.

The Cephalic Index.—Anthropologists have employed the shape of the head as a character in classifying the races of mankind. The **cephalic index** is used to express the shape of the head. It states the proportion that the breadth bears to the length of the skull (Figs. 145, *A*, *B*). The length or **long diameter** of the skull is usually measured from the glabella to the most projecting point of the occiput—commonly situated over the occipital poles of the brain; the breadth or widest diameter is measured between the widest points—usually some distance below the parietal eminences. If the length of a skull is 100 mm. and the breadth 75, the cephalic index of that skull is 75, *i.e.* the breadth is 75 % of the length. Human races, on an average, are either **Dolichocephalic** (long-headed), the breadth being 75 % or less of the length; **Brachycephalic**, in which the breadth is 80 % or more of length; or **Mesaticephalic**, in which the breadth is between

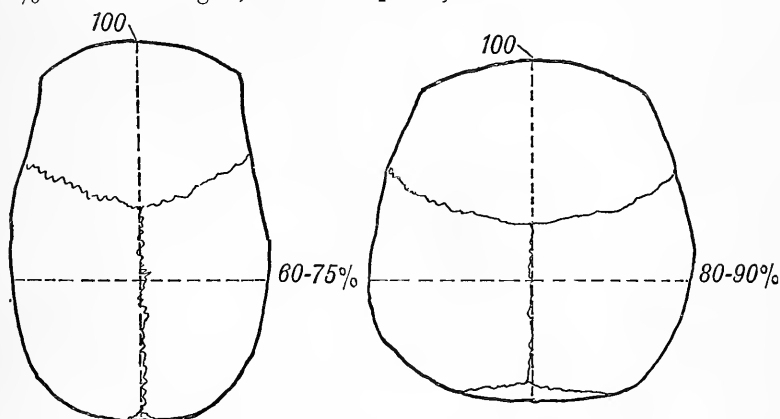


FIG. 145, *A*.—Diagram of a Long-head (Dolichocephalic).
B.—Diagram of a Short-head (Brachycephalic).

75 % and 80 % of the length. Various methods are employed in estimating the height of the skull, but the best is that which takes the upper margin of the external auditory meatuses as representing the basal plane. The height is measured from this plane to the highest point in the sagittal suture, when the skull is oriented so that the lower border of the orbit and the middle of the meatus are in one plane (see Duckworth, *Morphology and Anthropology*).

The English people have an average cephalic index of 78, the South Germans 83, but it must be remembered the individuals of every race show a wide range of variation. It will be seen that the topography of the brain, worked out by German surgeons, cannot be applied to the longer English heads without modification.

Factors which determine the Shape of Head.—The shape of the skull depends (1) on the size and shape of the brain; (2) on the size and strength of the muscles which arise from it—the muscles of mastication, or are inserted to it—the muscles of the neck. Brain growth is by far the most important factor, but we do not know the conditions which flatten the brain from side to side in dolichocephalic races, or shorten it from

frontal pole to occipital pole in brachycephalic races. Muscular action can only exercise a minor effect. Professor Arthur Thomson¹ has shown that there is a correlation between dolichocephaly and the size of the temporal muscles—which are relatively large in long-headed races—and the shape and mechanism of the mandible. It is to be remembered that (1) the muscles of mastication and of the neck undergo their greatest development between the 12th and 28th years; (2) before that time the brain has almost completely attained its adult size and shape; (3) all the evidence obtained from measurements in the living indicates that the changes in

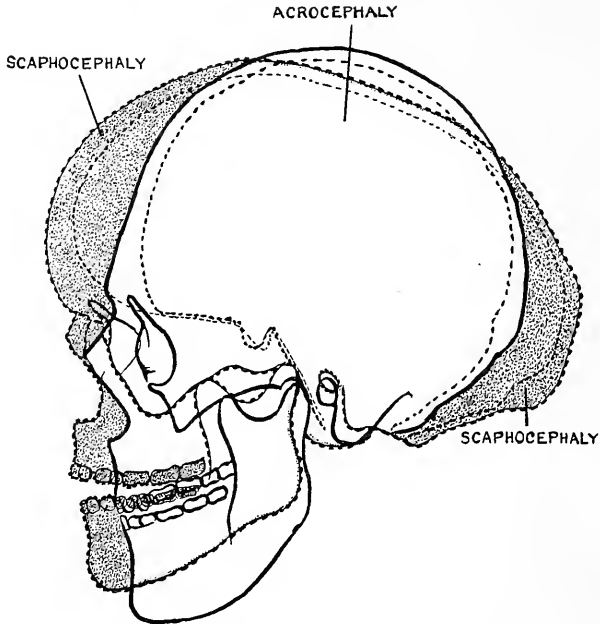


FIG. 146.—Outlines of Abnormal Skulls, showing a contrast in shape.

cranial form which take place then affect its external contour, leaving the shape of the cranial cavity unaffected.

Abnormal Crania.²—It is possible that light will be thrown on the factors which determine head-form by the study of certain pathological conditions. In the disease known as Acromegaly, where there is always a great enlargement of the pituitary gland, the skull undergoes peculiar growth changes. The supra-orbital ridges become greatly developed, the face elongates, the temporal lines from which the temporal muscles arise, grow upwards on the side of the skull, thus increasing the area of the temporal muscles. At the same time the lines which mark the attachment of the muscles of the neck—the mastoid processes, superior curved

¹ Arthur Thomson, *Man's Cranial Form*, Oxford, 1903.

² For skull in achondroplasia see Dr. Murk Jansen, *Achondroplasia*, Leyden, 1912; A. Keith, *Journ. Anat. and Physiol.* 1913, vol. 47, p. 189. For Acromegalic changes: Keith, *Lancet*, 1911, vol. 1, p. 993.

lines and external occipital protuberance—also increase greatly in size. In achondroplasia and in rickets the skull assumes characteristic forms due to a disturbance in the growth of the base of the skull. To a certain degree the growth of the cranial bones is regulated by internal secretions. In Fig. 146 two common types of abnormal skull forms are shown. They are contrasted types; in one—Acrocephaly or steeple-skull—the base is abnormally short, owing to an arrest of growth at the junction of the pre-sphenoid and ethmoid. Compensation is obtained by an upward growth of the brain, thus heightening the roof. In severe cases the optic nerves may be pressed on, and blindness thus caused. In the second type—Scaphocephaly, or boat-shaped skull—the cranium is very narrow from side to side, while the calvarial arc—from nasion to opisthion (posterior border of foramen magnum)—is greatly elongated. In scaphocephaly there is an

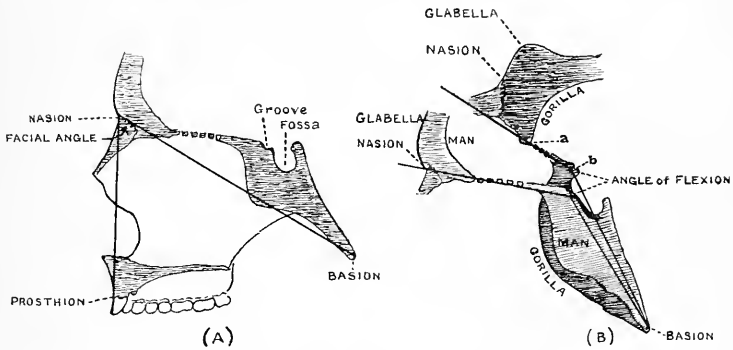


FIG. 147, A.—The Facial Angle as estimated by two lines drawn from the Nasion to the Basion and to the Prosthion (incisor alveolus).

B.—Method of estimating the degree of flexion and extension of the cranial axis. *a*, anterior border of cribriform plate; *b*, on olivary groove in front of olivary eminence. *a*, *b*, trabecular axis; *b*—basion—the chordal axis. The angle of flexion is contained by the two lines meeting at *b*.

arrest of growth—often a synostosis—along the sagittal suture. In acrocephaly the coronal suture is closed. In these two, and in allied conditions, there is a certain amount of evidence which points to a disturbance in the function of the glands of internal secretion.

The Facial Angle¹ is the angle at which the face projects from the axis of the skull (Figs. 147, 148). The skull consists in man, as in all mammals, of two parts—the facial part (splanchnocranium), which carries the teeth and is developed according to their size, and the **brain capsule** (neurocranium), which depends on the size of the brain. The smaller the brain and the larger the face, the more does the face project in front of the skull, and, therefore, the greater is the facial angle, and *vice versa*. It will thus be seen that the facial angle is to a certain degree an index of brain development. It is smallest in the most highly developed races of man; it is larger in the lower races, and larger still in the anthropoids; it increases in size with the

¹ For a description of the various methods of estimating the facial angle see Duckworth's *Morphology and Anthropology*, 2nd Edition, 1915.

advent of the permanent teeth and the necessary increase in the size of the face. It is, therefore, greater in the adult than in the newly born.

Flexion of the Cranial Axis.—In Figs. 147, *A*, and 148 the axis of the cranial base is represented by a line drawn from basion to nasion, but it is quite apparent that this line does not represent the axis accurately. The truth is that there are two parts in the cranial axis which are functionally as well as morphologically distinct, the chordal and prechordal parts (p.136). In the higher primates—especially in man—the prechordal part is bent downwards—or flexed—on the chordal. The manner in which the degree or angle of flexion may be measured is shown in Fig. 147, *B*; it is a much opener angle in anthropoids than in man. The degree of flexion is most

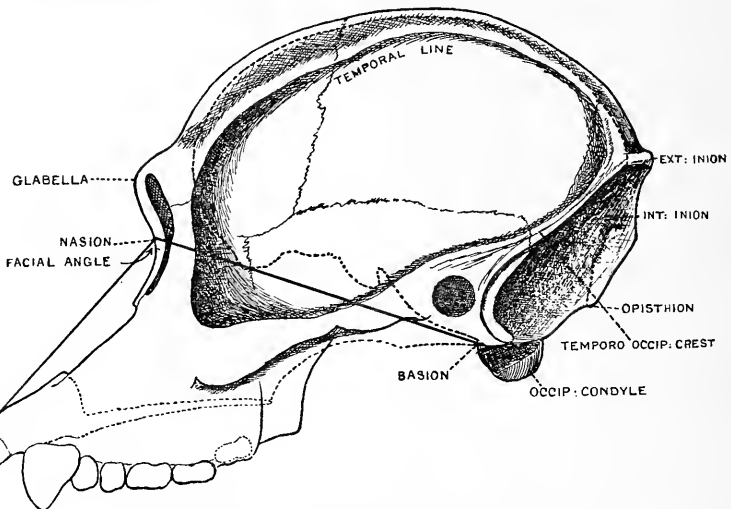


FIG. 148.—Profile of the Cranium of an Immature Chimpanzee, showing the ascent of the Temporal Ridges, the formation of Occipital Crests and the lines of the Facial Angle.

variable in man; in cases where the flexion is great the forehead is projecting and the face receding, the facial angle being apparently small. If there is a great degree of extension of the axis, then the forehead is receding, and the lower part of the face projecting or prognathous. Thus the facial angle is not a safe guide to the degree of prognathism or face projection, because it may be exaggerated or masked by the extension or flexion of the cranial base.

The Para-occipital Process is sometimes present in man, and projects downwards from the jugular process of the occipital bone. The rectus capitis lateralis is inserted to it. The process represents the para-occipital process, which is so highly developed in four-footed mammals. The *paramastoid* process projects from the temporal bone lateral to the para-occipital (Parsons).

Ungrowth of the Temporal and Occipital Ridges or Curved Lines.—In lower animals, such as the ape or dog, a great increase in the develop-

ment of the temporal and nuchal muscles takes place with the eruption of the permanent teeth, the area of their origin from the skull being necessarily enlarged. The ridges of bone which mark the limit of attachment of these muscles, the temporal and occipital ridges, ascend on the skull as waves of bone before the growing muscles. The ridges may meet, as in apes, along the sagittal and lambdoidal sutures and form great crest-like upgrowths. In Fig. 148 the position of the temporal lines in a juvenile chimpanzee is shown; they are approaching the sagittal suture. They have extended backwards, and met with the occipital lines, which are ascending above the attachment of the growing muscles of the neck. The temporal and occipital lines are seen to be fused together to form a temporo-occipital crest. At the same time the temporal lines spread forwards on the frontal region, the frontal extension being accompanied by a marked growth of the supra-orbital ridges and of the zygomatic arches. Thus the

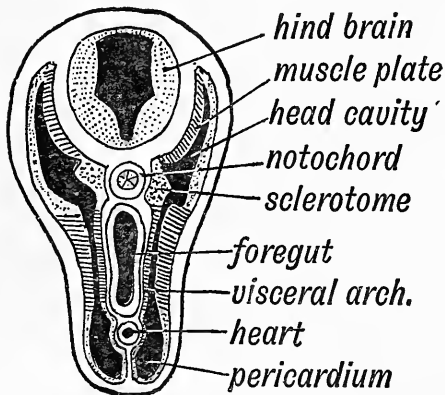


FIG. 149.—Scheme of a Segmental Head Cavity and of the various parts formed from it.

skull is modified by the growth of the muscles of mastication and of the neck. In man these changes also take place, but to a less extent than in anthropoids. At birth the temporal lines are just above the lower border of the parietal bones. During the second year the mastoid part of the ridge for the attachment of the neck muscles grows downwards into a pyramidal process—the mastoid—which is peculiar to the human species. In Neanderthal man, the mastoid process is shaped as in anthropoids.¹

Segmentation Theory of the Skull.²—It is inferred from investigations made on the developing heads of fishes and amphibians that each

¹ See Keith, *Journ. Anat. and Physiol.* 1910, vol. 44, p. 251.

² Some researches on the morphology and segmentation of the skull are: W. H. Gaskell, *Origin of Vertebrates*, London, 1910; E. S. Goodrich, *Proc. Zool. Soc. Lond.* 1911, p. 101; W. E. Agar, *Proc. Roy. Soc. Edin.* 1907, Feb. 4th; Schumacher, *Anat. Anz.* 1907, vol. 31, p. 145; Gaupp, *Verhand. Anat. Gesellsch.* 1907, p. 129; Greil, *ibid.* p. 59; F. H. Edgeworth, *Quart. Journ. Mic. Sc.* 1911, vol. 56, p. 167, *Journ. Anat. and Physiol.* 1903, vol. 37, p. 73; J. W. van Wijhe, *Petrus Camper.* 1906, vol. 4, p. 1; A. Meek, *Journ. of Anat. and Physiol.* 1911, vol. 45, p. 357 (*Dev. Skull of Crocodile*); W. Wright, *Lancet*, 1909, vol. 1, p. 669 (*Morphology and Variations of Skull*). See also references on p. 135.

primitive cephalic segment contains a cavity comparable to that seen in each body segment (p. 67), from the wall of which are developed (see Fig. 149): (1) a sclerotome, (2) muscle plate, (3) skin plate, (4) modified nephrotome, (5) a ventral part of the walls join in the formation of the coelom. A part of each segment, on the lateral aspect of the fore-gut, is modified to form a visceral arch (Fig. 149). The sclerotome of each segment forms (1) a cartilaginous sheath for the notochord, (2) a cartilaginous roof for the neural tube, (3) a process which runs into the branchial part of the segment. The number of segments in the mammalian head is by no means settled; on the evidence of the cranial nerves the number appears to be seven (p. 98), but certain considerations, specially relating to the facial and branchial structures, which we proceed to examine in the next chapter, lead us to suspect that the number is nine—the number of neuromeres which are marked out on the hind-brain.

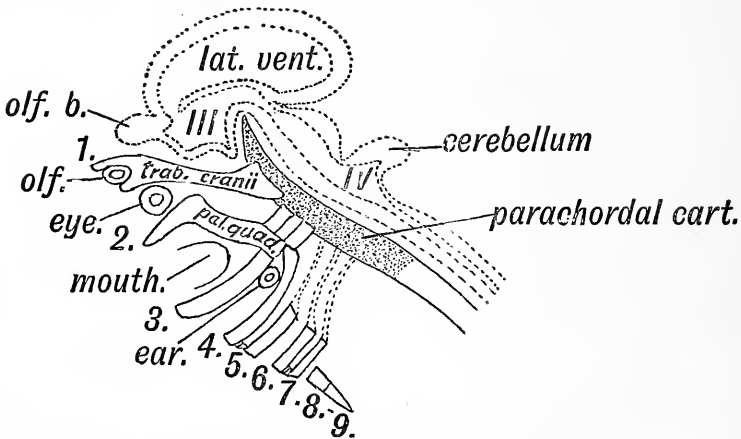


FIG. 150.—A schematic diagram of the segmental elements of the Skull. The numbers refer to the Cartilaginous Bars of the various Visceral Arches. The 4th and 5th are combined in the Hyoid Bone, the 6th and 7th in the Thyroid Cartilage, the 8th (and 9th?) in the Arytenoid, Cricoid, and Tracheal Cartilages.

In Fig. 150 a diagrammatic representation is given of one of the many segmental theories of the skull. The parachordal plate represents the unseparated centra of the nine segments. The primitive neural arches have been disturbed by (1) the enormous enlargement of the neural tube, but especially by the expansion of that tube in front of the notochord and parachordal plate to form the cerebrum and basal ganglia. In amphioxus the neural tube does not extend beyond the notochord. All that remains of the neural arches of the nine primitive segments are the lateral occipital cartilaginous processes (Fig. 139). Of the cartilaginous processes of the nine segments the 1st form the trabeculae cranii (Huxley, Howes); with the forward protrusion of the neural tube these come to form part of the base of the skull; the 2nd form the palato-quadrates. Both of these processes are preoral. The 3rd forms the mandibular bar, the 4th the hyoid bar, the 5th, 6th, 7th, 8th form the cartilaginous bars in the 1st, 2nd, 3rd and 4th branchial arches. The reader will see that if the first and last

cartilages are rejected as having no segmental significance, the theory put forward here is identical with that formulated in connection with the cranial nerves. We are at least justified in assuming that the parachordal part of the skull is the oldest, and is therefore known as the **palaeocranium**; whereas the prechordal part is more recent and is for this reason known as the **neocranium**. Further details relating to the facial and pharyngeal parts of the head will be given in the following chapters.

Gaskell's Theory.¹—Gaskell regarded the trabecular or prechordal part of the vertebrate head as a derivative of the prosoma, and the parachordal part from the mesosoma of an invertebrate form such as is now exemplified by the Kingcrab (*Limulus*). The prosoma carries 7 pairs of appendages which surround the mouth. The last of these represents the mandible, the first, the nasal processes; the intermediate appendages are combined in the maxillary processes. The mesosoma carries processes which serve for respiration and locomotion. In vertebrates these are modified to form branchial arches.

¹ See *Origin of Vertebrates*, London, 1910.

CHAPTER XII.

DEVELOPMENT OF THE FACE.

Evolution of the Human Face.—In our survey of the neural part of the human cranium we have seen that its outstanding features are the result of a great cerebral development. When, however, we turn to the facial and pharyngeal parts of the skull and head, we find that the factors which have determined their shape are related to the functions of smell, respiration and of mastication. It is unnecessary to again insist on the fact that the human embryo, in the latter part of the first month, shows a resemblance to a generalized type of fish; it possesses the basis of a branchial arch system. As in the fish, the olfactory organ is represented by

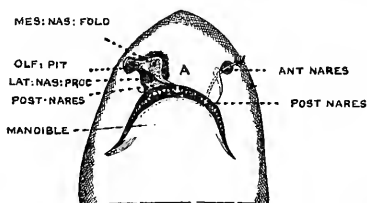


FIG. 151.—The Naso-Buccal Grooves of a Dog-Fish. On the right side the naso-buccal channel is exposed.

a pair of pits or depressions, which at first have no communication with the mouth. In some forms of fish—certain rays and sharks (Fig. 151)—a channel is formed between each olfactory pit and the mouth. The functional meaning of such a channel is evident; the water imbibed is sampled by the nose before entering the mouth. When pulmonary breathing was introduced, as in Dipnoean fishes, the open naso-buccal channel became enclosed by the union of its bounding folds. In amphibians, reptiles and birds the naso-buccal channel becomes dilated to form a true respiratory nasal passage, and the parts bounding the passage unite on the roof of the mouth to form the **primitive palate**. In Fig. 152 the parts entering into the formation of the primitive palate are shown. They are three in number: (1) a premaxillary and vomerine part developed between the nasal passages; (2) a right and left maxillary part, laid down on the lateral or outer aspect of each passage. In mammals a fourth element is added to the primitive or reptilian palate, and in this way the mammalian mouth is separated from the nasal respiratory passage, and can serve the purposes of mastication and suction. Thus in the evolution of the face

there have been three distinct stages: (1) a piscine, in which the nose and mouth were formed independently; (2) an amphibian stage, where the nasal respiratory passage opened on the roof of the mouth; (3) a mammalian stage, in which it opened in the naso-pharynx. In the development of the human embryo we see these three stages reproduced.¹

Processes which form the Face.²—Towards the end of the 4th week of foetal life, five processes begin to spring from the base of the primitive cerebral capsule, which by the end of the second month have completely united together to form the facial part of the head. In Fig. 153, a diagrammatic representation is given of the condition of these five processes about the end of the 6th week of development. Of the five, one, the

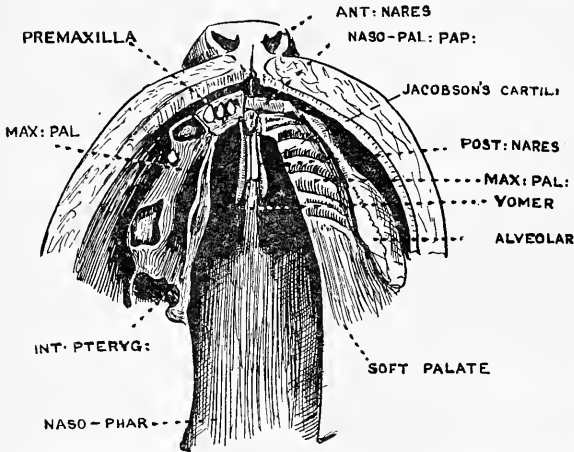


Fig. 152.—Roof of the Mouth of a Lion-Pup, showing the condition of Cleft Palate recalling in form the Palate of Reptiles. On the right side the bones are exposed by removal of the soft parts.

nasal or fronto-nasal, composed of symmetrical right and left halves, is median, and projects beneath the fore-brain; the others are lateral, two on each side, the **mandibular** and **maxillary**. The cavity which these five processes surround is the **stomodaeum**, a space ultimately destined to form the nasal and part of the buccal cavities. The representatives of these five elements are recognizable in certain fishes (see Fig. 151). The part of the adult face formed by each process is shown in Fig. 154.

Nasal Region of Face.—In reality the core of the face is formed by the cartilaginous capsule which encloses the organ of smell. We have seen that the olfactory capsule occupies the terminal part of the prechordal plate, and in primitive vertebrates forms the entire snout or face (Figs. 130, 133). Hence the first step in the development of the human face represents the upbuilding of the nasal cavities. Three stages in this process

¹ See Professor J. E. Frazer, *Lancet*, 1916, vol. 2, p. 45; Berry and Legg, *Harelip and Cleft Palate*, 1918; Keith, "Malformations of the Head and Neck," *Brit. Med. Journ.* 1909, vol. 2, p. 310.

² K. Peter, *Anat. Anz.* 1911, vol. 39, p. 41 (Development of Face).

are depicted in Fig. 155, taken from a recent research by Professor Frazer.¹ At the end of the 5th week the olfactory organ is exposed on each side of the fore-brain as a plaque surrounded by a growing raised margin or fold. The pituitary recess, opening from the stomodaeum (Fig. 155, *A*) lies in contact with the under surface of the fore-brain. At the end of the 6th week (*B*), the olfactory plaque has become a pocket by the upgrowth of the mesial and lateral nasal folds or processes which, being united above, rise up as a hood. Below, the olfactory pit communicates with the buccal cavity by an open naso-buccal channel—just as in the dog-fish. At the same time the maxillary process grows forward, and applies itself to and fuses with the substance of the lateral nasal fold. In the 7th week (*C*) the maxillary process has come in contact and fused with the globular end

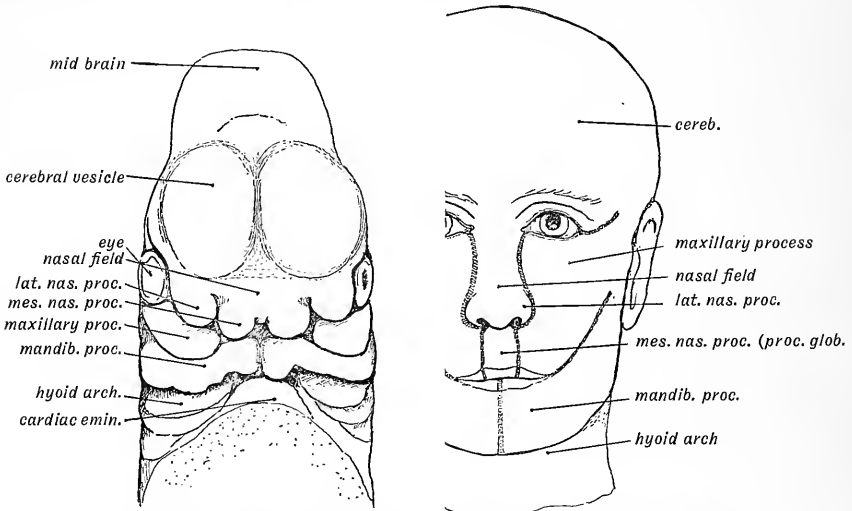


FIG. 153.—Showing the formation of the Face by the Nasal, Maxillary and Mandibular Processes in an Embryo of the 6th week. (After His.)

FIG. 154.—Showing the parts of the Face formed from the Nasal, Maxillary and Mandibular Processes.

(globular process) of the mesial nasal fold, and thus the naso-buccal channel is covered over and we can now speak of anterior nares and a posterior opening or primitive choana—at first closed by an epithelial membrane (Fig. 155, *C*). As the olfactory pockets enlarge they come closer together under the fore-brain until the mesial folds and the tissues between them form the primitive septum of the nose—the lateral nasal fold and intermediate tissue of each side being sometimes called by a separate name—the fronto-nasal process. Thus the nasal cavities which form the foundation of the face are built against the wall of the fore-brain and the nasal folds represent the margins of the outgrowing edifice.

Malformations of the Face.—These processes may fail to unite in the second month, and in this manner malformations of the face are produced. The most common anomaly is a partial failure of the nasal and

¹ See references, p. 165.

maxillary processes to fuse, various degrees of **hare lip** and **cleft palate** being thus caused. In **hare lip**,¹ the cleft appears in the upper lip between the middle part formed by the mesial nasal processes and the lateral parts formed by the maxillary processes (Fig. 154). In **cleft palate**, the failure of union occurs between the deep parts of the nasal and maxillary processes (Fig. 171). The lateral or the mesial parts of the nasal process may fail to fuse with the maxillary processes, and these appear on the face as polypoid or irregular projections (Figs. 156, 157). In such cases the right and left maxillary processes may unite and form the whole of the upper lip. **Macrostoma** is due to a partial failure of the mandibular to unite with the maxillary element. Any of these processes may be under-

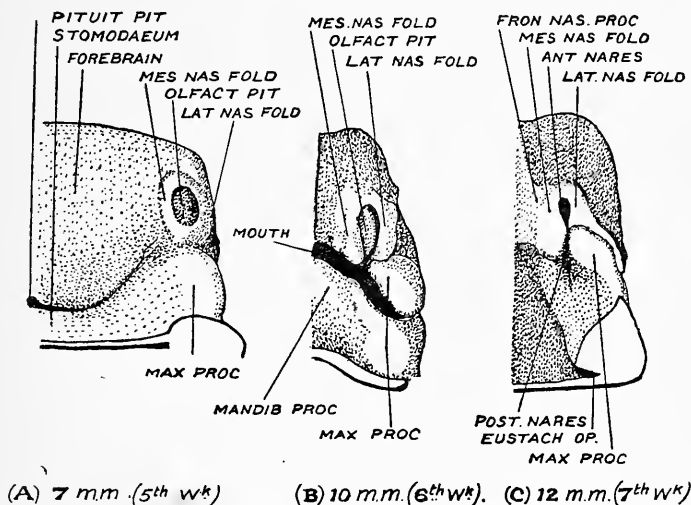


FIG. 155.—Three stages in the formation of the Nasal Cavities and Primitive Palate. (Prof. J. E. Frazer.)

or over-developed; over-development of the nasal and under-development of the mandibular (micrognathia) are of common occurrence.

The **cleft in the lip** of the hare is exactly in the middle line, and is due to a separation of the right and left parts of the mesial nasal process. The condition of **median hare lip**, which is rare in man, is represented in Fig. 158; in this case there was a partial cleft of the palate, and the pituitary body formed a tumour-like mass within the septum of the nose. A median cleft in the lower lip is also rare, and is due to a failure in the union of the right and left mandibular processes of the lower jaw (Fig. 159). Another remarkable condition—**cyclopia**—is shown in Fig. 202, p. 202, where the nasal processes have united together to form a single proboscis-like structure projecting above the eyes, which are partly fused.

¹ For an account of the development of the lips see: L. Bolk, *Anat. Hefte*, 1911, vol. 44, p. 227 (describes curious pits seen in abnormally developed lower lips); M. Ramm, *Anat. Hefte*, 1905, vol. 29, p. 55; W. L. H. Duckworth, *Journ. Anat. and Physiol.* 1910, vol. 44, p. 349 (Lips of Primates).

In this condition the palate and upper lip are formed by the union of the maxillary processes. The condition is not uncommon, and shows how adaptable the various embryological parts of the face are.¹

The Method of Fusion.—The manner in which embryological parts unite is similar in nature to the healing of wounds. Fig. 160 represents

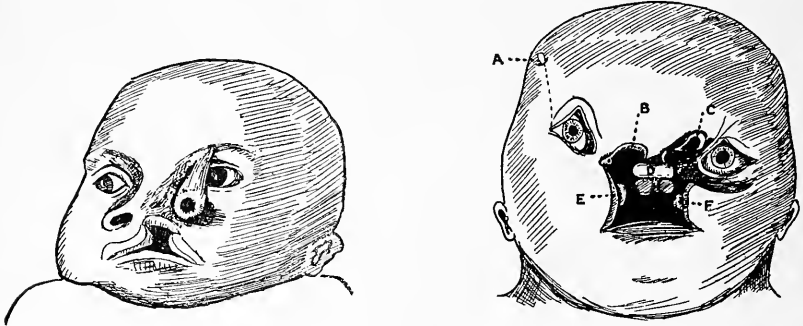


FIG. 156.—Face of a Child showing the left Nasal Process and Pocket as a free Poly-poid Body and the left Maxillary Process ununited with the Mesial Nasal (left Hare Lip). (After Kirchmayer.)

FIG. 157.—Face of Child in which the Nasal and Maxillary Processes are ununited. A, Polypoid Tubercle in line of Naso-Maxillary Cleft; B, Right Lateral Nasal Process; C, Left Lateral Nasal Process; D, Mesial Nasal Process; E, F, Maxillary Process. (London Hospital Medical College.)

a coronal section of the head of a human embryo, in which the mesial nasal process containing the germinal epithelium of the upper incisor teeth is about to unite with the maxillary. The ectodermic coverings of the processes are in contact. Across the epithelial union thus formed

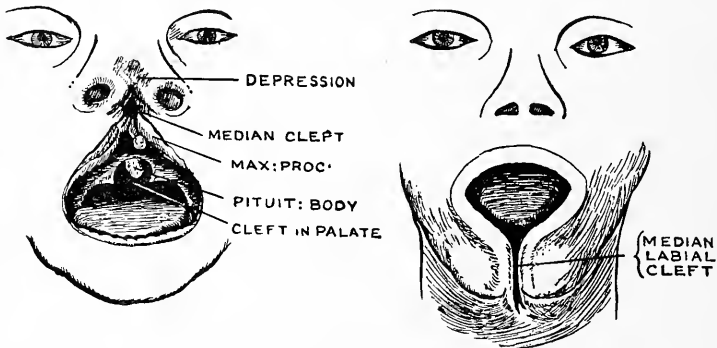


FIG. 158.—Median Hare Lip in a Child with Partial Cleft Palate and Ectopia of the Pituitary. (Mr. A. R. Tweedie's case.)

FIG. 159.—Median Cleft of the Lower Lip and Jaw. (Prof. MacCormick's case.)

the mesodermal tissue spreads, the two processes thus becoming intimately united. We know that the process of healing may be arrested by many pathological conditions; the process of embryological union may be also

¹ F. P. Mall, *Contributions to Embryology*, 1917, vol. 6, No. 15; R. J. Gladstone, *Journ. Anat.* 1920, vol. 54, p. 196; Davidson Black, *Journ. C. Neur.* 1913, vol. 23, p. 193.

arrested, but the exact causes of the arrest we do not yet know. If union of the facial processes fails to take place, then subsequent growth tends to move the processes apart, and union becomes impossible. The cleft in the lip or palate increases in width as the foetus becomes older. The tongue lies between the maxillary plates (Fig. 161), a normal position during the 2nd month. It is extruded as the palate is formed, the extrusion being due to the rapid growth of the mandibular and maxillary processes in the earlier part of the 3rd month.

Structures formed in the Mesial Nasal Processes.—We have already seen that the mesial nasal processes, which represent the inner walls of the nasal pockets or cavities, grow out from the base of the fore-cranium, and when they grow together to form the primitive septum of the nose, the cartilage formed in their united substance represents a direct forward

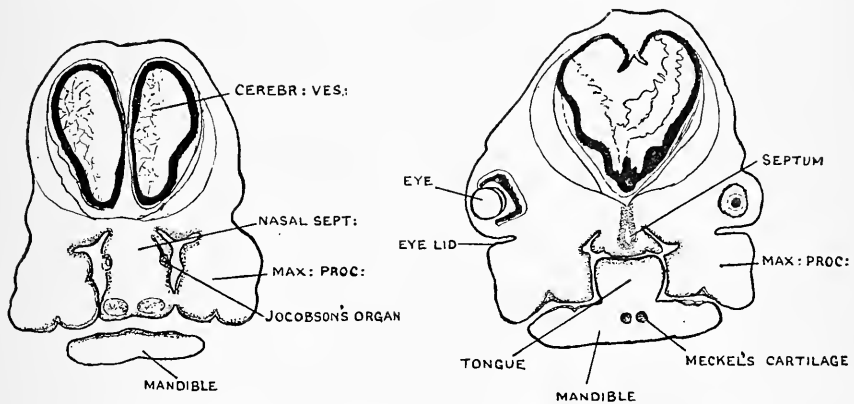


FIG. 160.—Coronal Section of the Head of a Human Embryo in the 6th week of development and 14 mm. long. (After J. L. Paulet, *Archiv. für Mik. Anat. und Entwickl.* 1911, vol. 76, p. 658.)

FIG. 161.—Similar Section of the same Embryo further back, showing the Tongue in the Palatal Cleft. (J. L. Paulet.)

continuation of the prechordal plate. From the united substance of the mesial nasal processes are formed the septum of the nose (Fig. 162), the premaxillary part of the upper jaw, and the middle third of the upper lip (Figs. 152, 157); in their anterior inferior angles are formed the premaxillae. The remainder forms the septum of the nose. Part of the cartilage of this septum remains unchanged as the septal cartilage (Fig. 162). In the septal wall are also developed the mesial limbs of the alar cartilages, which give form to the anterior nares. One element is added to the lower anterior part of the septum—just above the opening of the naso-palatine canal—the paraseptal cartilages (Fig. 142) which primarily serve for the protection of an isolated area of the olfactory membrane—Jacobson's organ—reduced to a vestige in man. In Fig. 155, *C* it will be observed that the lateral nasal process also fuses with the mesial; the paraseptal cartilages are derived from the lateral nasal processes (Fawcett).

The vomer is developed in the membrane (perichondrium) which covers the primitive septum (Fig. 169). A centre of ossification appears at the

end of the 2nd month on each side near the lower border of the septum ; these fuse together under the palatal margin of the cartilage. Thus the vomer forms at first a shallow trough in which the cartilage of the septum appears to be implanted (Fig. 163).

The **Vertical Plate of the Ethmoid** is formed by a direct ossification of the cartilage of the primitive septum. Ossification begins in the 4th month.

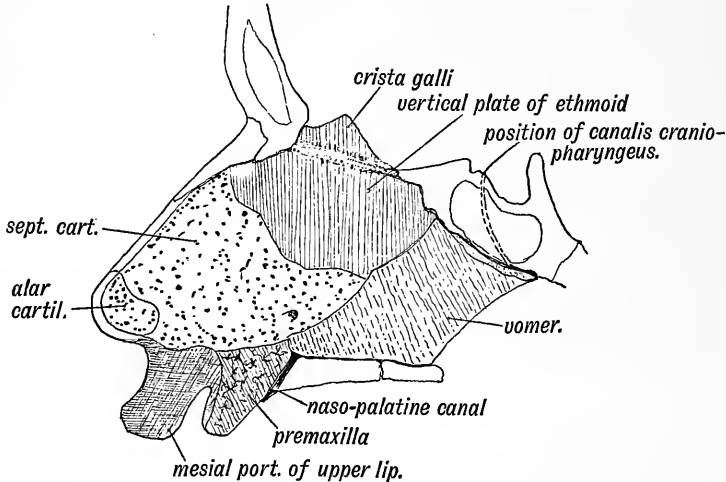


FIG. 162.—Showing the structures formed in the Mesial Nasal Processes.

The crista galli, the intra-cranial part of the septum, is formed in part by the ossification proceeding into the attachment of the falx cerebri.

Premaxillary Bones.—The two premaxillary bones form the sockets of the four upper incisor teeth. In the human foetus at birth the suture between the premaxilla and maxilla can be seen on the hard palate ; it runs on each side from the naso-palatine foramen to the alveolus between

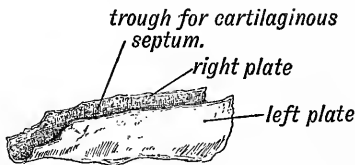


FIG. 163.—Showing the Trough-shaped Vomer of the newly-born.

the lateral incisor and canine (Fig. 165). As is illustrated in Fig. 165, the relationship of this suture to the tooth sockets is variable, but the relationship just mentioned is the usual one. On the facial aspect, a suture between the premaxilla and maxilla is at no stage distinct, the maxillae appearing to overlap the premaxillary elements, almost completely excluding them from the face. The nasal spine is formed by the premaxillae. The palatal plates of the premaxillae represent the prevomers which are seen as distinct bones in the primitive palate of amphibia.

In mammals generally the premaxillae are highly developed, separated throughout their whole extent by a suture from the maxillae and form the snout part of the face. In the higher Primates the face becomes less elongated, less **prognathous**, or projecting, and the premaxillae less developed. In the orang, for instance, the premaxillary sutures are distinctly seen on the face at birth (Fig. 164), but as the permanent canines begin to develop they fuse with the maxillae. The premaxilla is more reduced in man than in any other primate; in him it is partly fused with, and overlapped by, the maxilla from the first appearance of ossification; in apes fusion does not occur until the eruption of the permanent teeth. The vestigial character of the premaxilla in man is due to the reduced size of his masticatory apparatus and the consequent retrogression in the development of the facial part of the skull.

Relationship of the Premaxilla to Cleft Palate.¹—It is usual for the sockets of all four incisor teeth to be formed by the premaxilla. In many

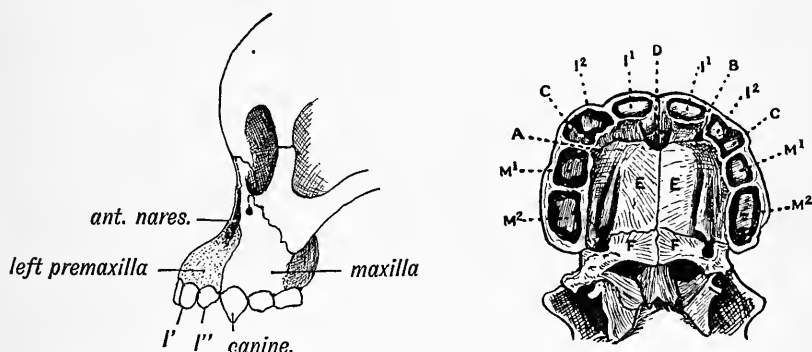


FIG. 164.—Showing the suture on the face between the premaxilla and maxilla in the Skull of a Young Orang.

FIG. 165.—Palate at birth, showing varieties of the suture between maxilla and premaxilla. On the right side (A) the suture between the palatal processes of premaxilla and maxilla ends at the socket of the canine; on the left (B) between the mesial (I¹) and lateral (I²) incisors; D, naso-palatine foramen, in which the anterior end of the vomer appears; E, F, palatal processes of the maxillary and palate bones.

cases of cleft palate (see Fig. 167) only the two central incisors are situated on the premaxilla, the sockets of the lateral incisors being attached to the maxilla. Even in the normal palate (Fig. 165, B) this may be the case. Albrecht supposed that each premaxilla was made up of two bones—an outer and an inner—and that in cleft palate the fissure might lie between the elements of the premaxillary or to their outer side. We now know (1) that cleft palate is not due to a failure of ossific centres to join, but to a non-union of two embryological masses—the mesial nasal and maxillary; (2) that the partial suture, which may divide the palatal part of the premaxilla, is due, not to two centres of ossification, but to the formation

¹ M. Inouye, *Anat. Hefte*, 1912, vol. 45, p. 471 (Premaxilla in Man); 1912, vol. 46, p. 1 (Dev. of Palate, Mammals); E. Gaupp, *Anat. Hefte*, 1910, vol. 42, p. 311 (Evol. of Palate); G. Schorr, *Anat. Hefte*, 1908, vol. 36, p. 69 (Dev. of Palate); E. Fawcett, *Journ. Anat. and Physiol.* 1906, vol. 40, p. 400 (Ossific. of Palate). See also references, p. 159.

of the palatal part by two processes—one corresponding to the middle incisor socket, the other to the lateral incisor; (3) the germ or bud of the lateral incisor is formed at the point of union of the mesial nasal and maxillary processes. If these processes fail to join, the bud of the lateral incisor, as the processes move apart during subsequent growth, may be carried away by the maxillary or premaxillary element, or, as I have seen, be left stranded in the cleft between the processes. If the lateral incisor remains attached to the maxillary process, then its socket is formed by that element; if by the premaxillary, then the cleft appears in the more usual situation, and the socket forms part of the premaxilla. The late Mr. Clement Lucas observed that the lateral incisor is often small or even absent in families subject to cleft palate.

Naso-palatine Foramen.—The naso-palatine foramina are formed where the mesial nasal and two maxillary processes unite to form the

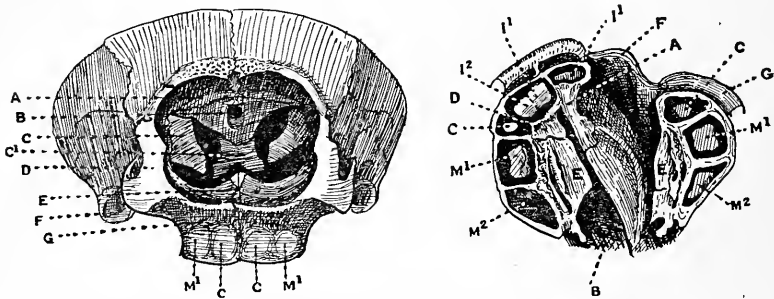


FIG. 166.—Facial part of the Skull of a Cyclops Foetus, in which the nasal processes formed a free proboscis, the eyes a median structure and the maxillary processes the palate. *A*, orbital plates of frontal; *B*, fused optic foramina; *C*, orbital plate of sphenoid; *C'*, basi-sphenoid; *E*, orbital plate of maxilla; *F*, ear; *G*, superior maxilla; *C*, canine; *M'*, first milk molar.

FIG. 167.—Case of Cleft Palate, in which the maxillary and premaxillary processes have remained ununited on the left side. *A*, septal process of premaxilla; *B*, nasal septum; *C*, canine; *D*, palatal process of premaxilla; *E*, palatal process of maxilla. The left lateral incisor was absent.

palate (Fig. 172). In animals with well-developed premaxillae the two naso-palatine (anterior-palatine) foramina are large, and through each passes the naso-palatine duct, which allows a communication between the buccal and nasal cavities. The odour of the food within the mouth thus reaches the organ of Jacobson, which is situated on the septum, close to the nasal orifice of the duct. In man the upper ends of the ducts remain open; they terminate blindly below, behind the mesial incisor teeth, in the naso-palatine or incisive papilla.

Nasal Duct.—The lachrymal sac and nasal duct, through which tears pass from the eye to the inferior meatus of the nasal cavity, are formed between the lateral nasal and maxillary processes (Figs. 154, 155, 157). At the end of the 6th week, when the furrow between the maxillary and nasal processes is obliterated, the nasal or naso-lachrymal duct is represented by a solid bud or core of ectoderm embedded at the inner angle of the eye and in the site of the upper part of the naso-maxillary groove or fissure. This bud becomes cord-like, one extremity growing towards the nasal

cavity, which it reaches at the beginning of the 3rd month, while the orbital extremity expands to form the lachrymal sac. The canaliculization of the duct begins in the 3rd month, but is not complete until late in foetal life. In Fig. 157 the lateral nasal and maxillary processes have not fused; the eye is separated by two folds from the nasal cavity; the outer represents the semilunar fold, the inner a fold in which the lachrymal canaliculi and caruncula lachrymalis are formed.

Structures formed in the Lateral Nasal Process.—The lateral nasal process is developed to form the outer wall and roof of the chamber containing the olfactory organ. Within it develops a plate of cartilage which represents the greater part of the cartilaginous olfactory capsule of lower vertebrates. In the human embryo the process of chondrification begins

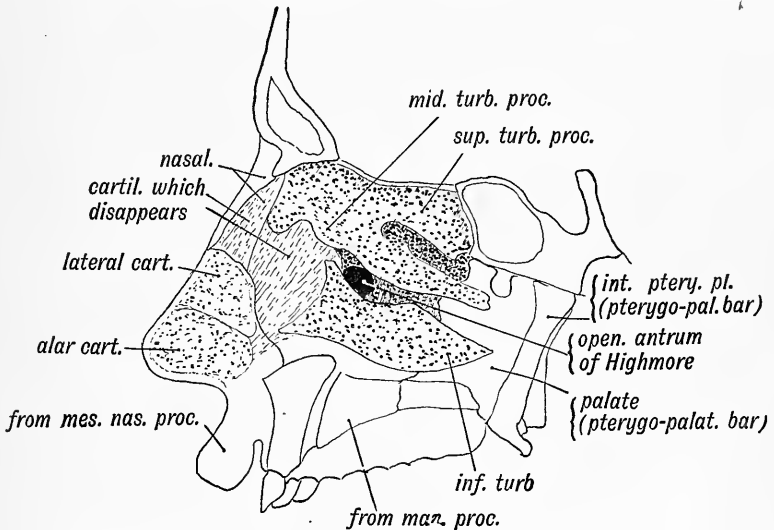


FIG. 168.—Showing the structures formed in the Lateral Nasal Processes.

near its lower border and spreads up towards the roof (Frazer), where it joins the upper edge of the septal cartilage, developed on the united mesial nasal processes and also spreads backwards to enfold the hinder part of the olfactory chamber and to become continuous with the presphenoid part of the prechordal plate. The cribriform area is the last to be formed (see Figs. 143, *A, B*, p. 148). In front, the lower border of the lateral nasal process joins the septal process, adding to it the paraseptal cartilage (p. 163).

What becomes of the Cartilage of the Lateral Nasal Process¹ (Fig. 168).—It forms on each side:

(1) The cribriform plate around the olfactory nerves as they issue from the olfactory bulb;

(2) The lateral mass of the ethmoid, at first merely a plate of cartilage; the superior and middle turbinate processes are developed from the plate

¹ See Fawcett, *loc. cit.* p. 135.

(Fig. 169); ossific centres appear in the cartilage of the lateral mass and turbinate processes during the fourth month of foetal life;

(3) The inferior turbinate bone (Fig. 169) (maxillo-turbinal). The body of the superior maxilla is developed on its outer side in the maxillary process (Fig. 169);

(4) The lateral and part of the alar cartilages of the nose;

(5) In the membrane over the cartilage, between the ethmoid behind and the cartilages of the nares in front, are developed the lachrymal and nasal bones, and the ascending process of the superior maxilla. The cartilage beneath these bones disappears after birth (Fig. 168). Ossification of the nasal bone appears at the beginning of the 3rd month; the

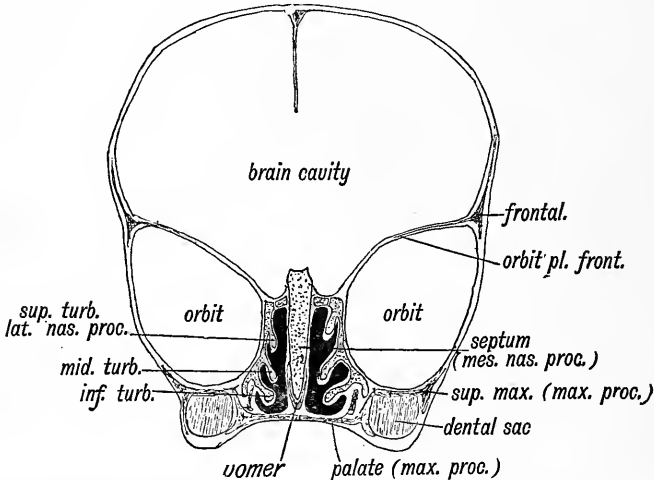


FIG. 169.—Coronal Section of the Skull of a 7th month Human Foetus to show the cartilages of the Lateral and Mesial Nasal Processes and the bones formed round them.

centre for the lachrymal appears late—at the beginning of the 4th month (Mall).

Arteries and Nerves of the Nasal Processes.—A knowledge of the development of the face assists one to unravel the complicated distribution of its arteries and nerves. Each process carries its own vessels and nerves.

1. **Mesial Nasal Process.** The chief artery and nerve of this process are the naso-palatine, but branches also come from the nasal nerve and its accompanying artery, the anterior ethmoidal.

2. **Lateral Nasal Process.** The nerves of the lateral nasal process are derived from Meckel's ganglion and from the descending palatine nerve. Vessels accompany these nerves from the descending palatine artery. The nasal nerve and anterior ethmoidal artery supply the process in front.

The Parts formed from each Maxillary Process.—The maxillary process springs from the base of the mandibular process at the end of the 4th week of development, and sweeping forwards below the eye, separates that structure from the mouth (see Figs. 44, 45, 154). In front it comes

in contact and fuses with the lateral nasal process, which it assists to form the outer wall and floor of the nasal cavity, and, in the 7th week, with the globular process of the mesial nasal which forms the premaxillary part of the palate and the middle part of the upper lip. The part of the face formed by the maxillary process is shown in Fig. 154. The hard palate (with the exception of the premaxillary part) is formed by a **palatal plate** which begins to grow inwards from the maxillary process in the 6th week (Fig. 170) and fuses with the plate of the opposite side about the 10th week. The palatal processes separate the buccal from the nasal cavities, forming the roof of the one and the floor of the other. The palatal plates meet first with the premaxillary part (Fig. 171); behind that they come in contact with each other; the process of fusion spreads backwards,

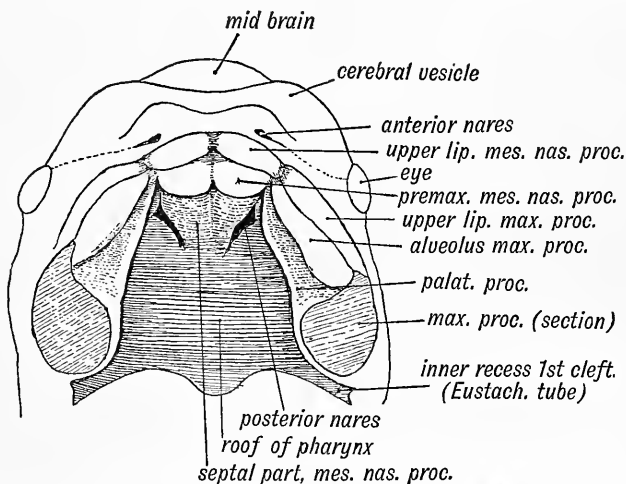


FIG. 170.—Showing the ingrowth of the Palatal Plates of the two Maxillary Processes at the end of the 6th week. The openings erroneously indicated as "posterior nares," are the primitive choanae. (After Kollmann.)

and before the end of the third month the hard and soft palates form a complete naso-buccal septum.

Cleft Palate.—To understand the manner in which the various forms of clefts arise in the palate it is necessary to note the manner in which the septum of the nose grows and the fate of the primitive choanae. At the end of the 6th week (Fig. 170) the nasal septum is seen to be relatively short and wide and to form the mesial borders of the primitive choanae or posterior nares (see Fig. 197). By the 9th week (Fig. 171) the septum has grown greatly in length, pushing the primitive palate forwards away from the base of the skull, and thus presenting a long posterior or palatal border which still forms the mesial edges of the primitive choanae; the choanae still extend from the primitive palate to the sphenoidal end of the septum. The dorsum of the foetal tongue lies against the palatal margin of the septum with the palatal folds tucked under its lateral margins (Fig. 161) until the 9th week, when the forward growth of the primitive palate lifts the nasal septum off the dorsum of the tongue and allows the

palatal folds to come in contact with each other and with the lower margin of the septum. The manner in which the palatal folds are applied to the septum is shown in Fig. 171, *B*; by a process akin to the healing of wounds the palatal folds unite with each other and with the palatal border of the septum. The process begins behind the premaxilla and passes backwards, but the posterior part of the septum is left free to form the partition between the permanent posterior nares. Thus in the formation of the palate a Y-shaped cleft has to be united; the short limbs lie on each side of the premaxilla in the primitive palate, the long limb in the middle line of the permanent or mammalian palate. All three parts may remain united as in Fig. 157, or the long limb with one short as in Fig. 167, or only the long limb as in Fig. 152. Further, it sometimes happens that one or both primitive choanae are closed permanently by the plug

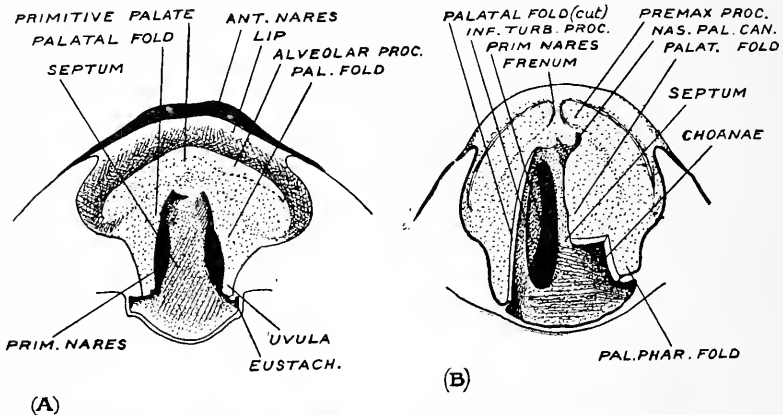


FIG. 171.—Development of the Maxillary Palate. *A*, stage reached in 9th week; *B*, schematic figure to illustrate the manner in which the maxillary folds are applied to the nasal septum. (Prof. Frazer.)

of epithelium which temporarily occludes them becoming organized and forming membrane or bone. As the septum and choanae expand this occluding membrane or partition is stretched and gives rise to **atresia of the posterior nares**. The wide gap and bent septum seen in nearly all cases of cleft palate are due to changes produced by growth in the later months of foetal life. An asymmetrical growth is a result of the failure in the union of the processes.

The Soft Palate.—While the hard palate is derived from the palatal plates of the maxillary processes, the soft palate (Fig. 171, *A*) is derived from a fold which arises as a prolongation backwards of each horizontal plate into the pharynx.¹ Into the **palatal folds** spread derivatives of the superior constrictor to form the palato-pharyngeus, palato-glossus and azygos uvulae, and possibly also the levator palati. The posterior pillars of the fauces are continuations of the palatal folds within the pharynx. A divided uvula represents a failure of the final stage in the formation of the palate.

¹ See J. Ernest Frazer, *Journ. Anat. and Physiol.* 1911, vol. 45, p. 190.

Bones formed in each Maxillary Process.¹—The zygomatic process of the temporal, the malar, and the greater part of the superior maxillary are formed directly in the connective tissue within the process. They are membrane-formed or **dermal bones**. The centre for the maxilla appears at the beginning of the 7th week in that part of the process which lies under the eye. Very soon, after the various processes of the face are fully united, an extension passes upwards over the lateral nasal cartilage towards the frontal bone (frontal process); the orbital, alveolar, and palatal processes are later extensions from the single centre of ossification (Mall, Fawcett).

Palato-Quadrate Bar.—In lower vertebrates the maxillary process is supported by a skeletal bar of cartilage known as the palato-quadrate bar, because it stretches from the palate to the quadrate bone, situated at the base of the mandibular arch (Fig. 173). Although in the human embryo this cartilaginous bar is at no time clearly differentiated (Fawcett), there

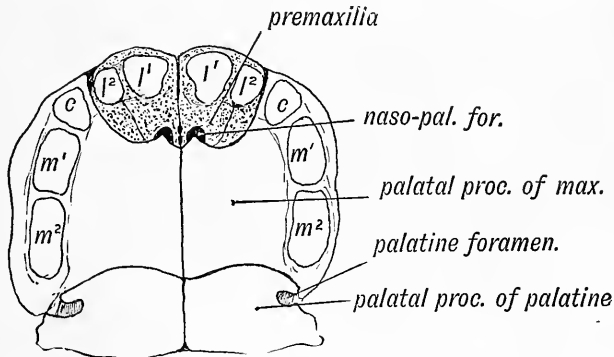


FIG. 172.—Showing the Hard Palate at birth. The premaxillary part is formed from the Mesial Nasal Processes; the remainder by the Palatal Plates of the Maxillary Processes.

can be no doubt that two bones have arisen in connection with it—namely the palate and internal pterygoid (Fig. 174). The internal pterygoid plate—the first part of the sphenoid to ossify—is formed early in the 3rd month in membranous tissue which overlies the position of the middle part of the bar, while the vertical plate of the palate is developed in membrane over its more anterior part. Ossification extends to the horizontal plate, within the horizontal plate of the maxillary process, at the end of the 2nd month.

The mandibular process has also a cartilaginous bar developed within it known as **Meckel's cartilage** (Fig. 173). Thus each of the processes which grow out to form the face has a basis of cartilage, but while the cartilages within the nasal processes are continuous with the base of the skull, the cartilage within the maxillary process comes in contact by its posterior extremity with Meckel's cartilage (Fig. 173). The quadrate bone, which is well seen as a separate element in birds and reptiles, forms a movable base on which the lower jaw articulates. This form of joint gives birds and reptiles an easy faculty of swallowing unmasticated food.

¹ E. Fawcett, *Journ. Anat. and Physiol.* 1911, vol. 45, p. 378 (Ossification of Maxilla). See also Mall, *Amer. Jour. Anat.* 1906, vol. 5, p. 449.

With the development of grinding and chewing teeth in the very early ancestry of mammals a more stable form of temporo-mandibular articulation was evolved, the mandible during the change coming to articulate with the temporal bone, thus leaving the upper end of Meckel's cartilage and the quadrate free to be utilized as the malleus and incus by the organ of hearing.

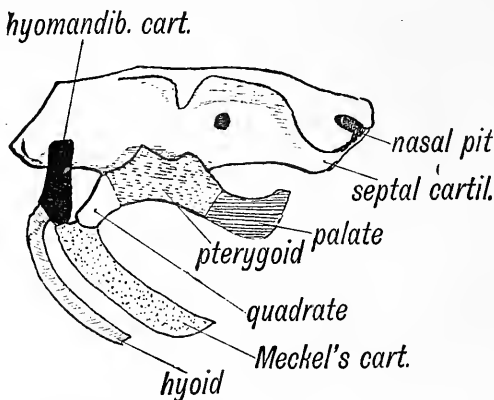


FIG. 173.—The Cartilages in the Nasal, Maxillary and Mandibular Processes of a Shark.

The simplest condition of the cartilages of the maxillary and mandibular processes is seen in certain fishes. In the common base of these two processes, there is developed a cartilage which binds the basal ends of the palato-quadrate bar and Meckel's cartilage to the skull. The cartilage of the hyoid arch is also bound to it, and hence it is known as the hyo-mandibular cartilage. (Compare Figs. 132, 133, 150 and 173.)

Nerves and Arteries of the Maxillary Process.—A knowledge of the manner in which the maxillary process is developed explains the distribu-

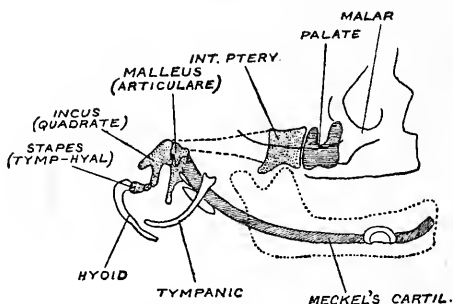


FIG. 174.—Diagram to show the position of the bones in the Skull of the Human Foetus which are formed in connection with the palato-quadrate bar.

tion and course of its arteries and nerves. The second division of the 5th, represented by the infra-orbital, descending palatine, pterygo-palatine, and Vidian nerves, forms its nerve supply. Its main artery is the internal maxillary.

Formation of Foramina and Canals in Bone.—The development of canals and foramina in the bones of the maxillary process illustrates the manner in which these are formed in the skull generally. Many foramina and canals occur between elements which unite in the course of development (see p. 150). The Vidian nerve lies between the internal pterygoid plate (a separate bone) and the external pterygoid, a plate which is formed in the maxillary process as a prolongation of the great wing of the sphenoid. The pterygo-palatine canal is situated between the pterygoid and palatal parts of the palato-quadrato bar. The descending palatine nerve lies between the palate bone and superior maxilla. These are canals formed between different elements. The infra-orbital nerve at first passes forwards in a groove on the orbital aspect of the superior maxilla, but in the later months of foetal life, upgrowths from the centre of ossification of the maxilla meet over the nerve and convert the groove into a canal.

The foramen rotundum and foramen ovale are at first notches on the edge of the great wing of the sphenoid, but in the course of foetal growth the notches are converted into foramina. Hence wherever a nerve foramen or canal is found one may conclude that it marks the junction of two elements, originally distinct, or that it is originally a groove or notch on the edge of the bone (Bland-Sutton). The foramina for nerves in the malar bone appear to be exceptions to this rule. Only one centre appears for the ossification of this bone (7th week), and the nerves evidently become involved during the ossification of the membranous basis. The malar bone is occasionally ossified from two centres which may fail to unite; the bone is then divided by a suture passing from the orbit to the temporal fossa. A divided malar occurs rather more frequently in Japanese and Mongolian skulls, hence the name of **Os Japonicum**.

Palatal Rugae.—In all classes of mammals the mucous membrane on the hard palate is ridged transversely; three or four of these transverse ridges are seen on each side of the palate of the newly born child; they tend to disappear in the adult. Food is triturated between them and the rough papillae on the palatal aspect of the tongue. Their disappearance in man is probably due to the soft nature of his food.

Maxillary Sinus.—It will be seen from Fig. 175 that the maxillary process is at first a thin plate, lying between the orbit and mouth, containing the canine and molar tooth buds. It rests on the outer aspect of the lateral nasal process, and to some extent assists that process to form the outer wall of the nasal cavity (Fig. 169). In the third month of foetal life the mucous membrane in the middle meatus begins to bud outwards, presses before it and bursts through the lateral nasal plate of cartilage and begins to distend the maxillary process. At birth the sinus is only a shallow recess on the outer wall of the middle meatus, above the germ of the first milk molar (Fig. 175). It continues to grow until the 25th year, and is the only one of the air sinuses developed from the nasal cavity which is more than a rudiment at the time of birth. In the years of adolescence the sinus expands until it inflates the maxillary part of the malar. As it expands backwards the posterior border of the maxilla, which contains the buds of the permanent molar teeth, undergoes a rotation

downwards, so that what was situated on the posterior border comes to be situated on the alveolar border (Fig. 176). If the processes of growth and rotation are arrested, the last molar (wisdom) tooth is left on the posterior border of the maxilla, where it may give rise to pain and supuration. The maxillary sinus or antrum is peculiarly large in man and

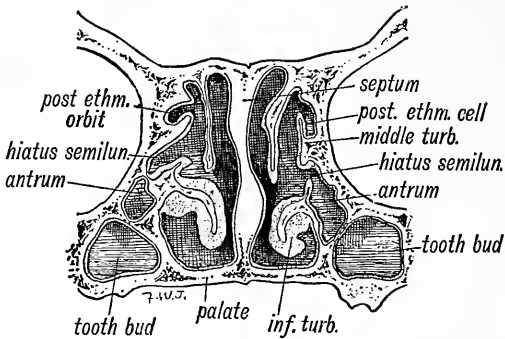


FIG. 175.—Coronal Section of the Nasal Cavities of a Newly-Born Child, showing the development of the hiatus semilunaris and air sinuses.

in the anthropoid apes. It is small in monkeys, a greatly expanded inferior meatus taking its place.¹

Mandibular Process and Arch.—The two mandibular processes unite in the middle line and form the mandibular or first visceral arch. The arch forms the lower or hinder boundary of the stomodaeum (Fig. 177). The right and left processes are in contact in the 4th week of development,

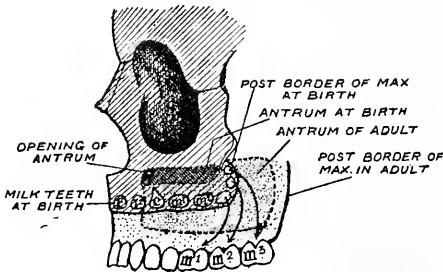


FIG. 176.—Showing the manner in which the development of the Maxillary Antrum affects the size of the palate and position of the molar teeth.

but the process of fusion, which may be arrested (Fig. 159), is not complete until the middle of the second month.

Parts formed from the Mandibular Arch.—Besides the lower jaw, there are formed from this arch the soft parts over and under the jaw, the lower lip, the muscles of mastication, the mylo-hyoid and anterior belly of

¹ See Keith, *Proc. Anat. Soc. Great Brit. and Ir.* May, 1902, *Brit. Journ. Dent. Sc.* 1902, vol. 45, p. 529; J. Parsons Schaeffer, *Amer. Journ. Anat.* 1912, vol. 13, p. 1; *Ibid. Amer. Journ. Anat.* 1912, vol. 13, p. 1 (Formation of Nasal Duct); *Ibid. Amer. Journ. Anat.* 1910, vol. 10, p. 313 (Formation of Antrum). See also references, p. 135.

the digastric, the tensor palati, and the tensor tympani. The anterior two-thirds of the tongue, the sublingual and submaxillary glands are formed from the floor of the primitive pharynx between the mandibular and the second or hyoid arch. These parts are supplied from the nerve of the mandibular arch, and are therefore probably derived, in part at least, from the substance of the arch. The whole arch and its derivatives are set apart primarily for the purpose of mastication. Only in mammals are the lips separated from the alveolar processes. In the human embryo the lower lip is demarcated from the alveolus by the downgrowth of an epithelial groove (the labio-alveolar plate or groove) about the middle of the 7th week.

The **Mandibular Arch** bounds the stomodaeum behind, and is the foremost of the visceral arches which encircle and form the walls of the primitive pharynx. **Meckel's cartilage**¹ forms its skeletal basis (Figs. 173, 174).

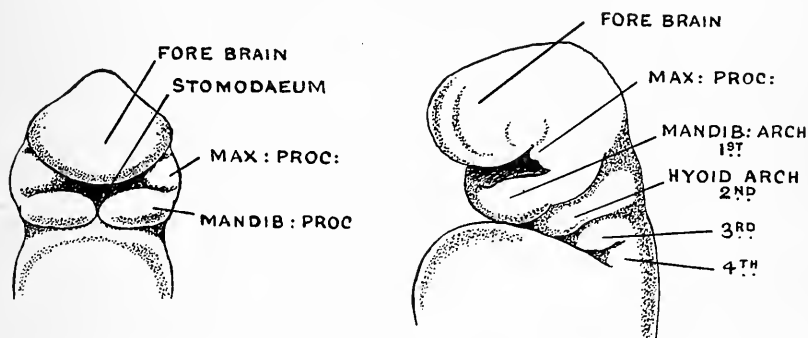


FIG. 177.—The Mandibular Arch and Stomodaeum (primitive mouth) in a Human Embryo of the 5th week. (After Rabl.) A, from the front; B, from the side.

The 3rd division of the 5th is its nerve, but its artery, the first aortic arch, has only a transient existence, although the inferior dental may represent part of it.

Development and Ossification of the Lower Jaw.²—In Fig. 178, which represents the condition of the human mandible at the beginning of the 4th month, the primitive cartilaginous skeleton of the mandibular arch can still be followed from the symphysis to the tympanum. Only one part of the cartilage takes a direct share in the formation of the mandible—that part which lies near the symphysis and assists to form the section of the mandible which carries the first premolar and canine teeth. The ventral extremities persist through foetal life as cartilaginous nodules; they may become ossified. The proximal end of Meckel's cartilage forms the malleus; all the rest of the bar disappears, although the long internal lateral ligament occupies the site of part of the cartilage. In rare instances

¹ E. Gaupp, *Anat. Anz.* 1911, vol. 39, pp. 97, 433, 609 (Morphology and Mandible).

² I have followed the account given by Dr. Alex. Low, *Journ. of Anat. and Physiol.* 1910, vol. 44, p. 83. See also Professor Fawcett's account in *Journ. Amer. Med. Assoc.* 1905, vol. 45, p. 695. For abnormal ossification of Meckel's cartilage see Keith, *Journ. Anat. and Physiol.* 1910, vol. 44, p. 151.

the cartilage may undergo complete and independent ossification. Thus the lower jaw, which shares with the clavicle the distinction of being the first bone in the body to ossify, is a membrane or dermal bone. Late in the 7th week a centre of ossification appears in each half, on the outer side of the Meckel's cartilage, and near the site of the future mental foramen. Each half of the lower jaw is ossified by the extension of a single centre. Processes grow up on either side of the inferior dental nerve which, with the tooth buds, comes to lie in a primitive alveolar trough. During the third month the ascending ramus begins to form. In the condylar and coronoid processes a formation of secondary cartilage occurs; thus the condyle and coronoid are ultimately laid down in cartilage. The two halves of the mandible unite at the symphysis during the second year; in some animals, such as the kangaroo, the symphysis remains open.

Evolution of the Mandible.—To interpret the appearances seen during the development of the human mandible we must suppose that Meckel's

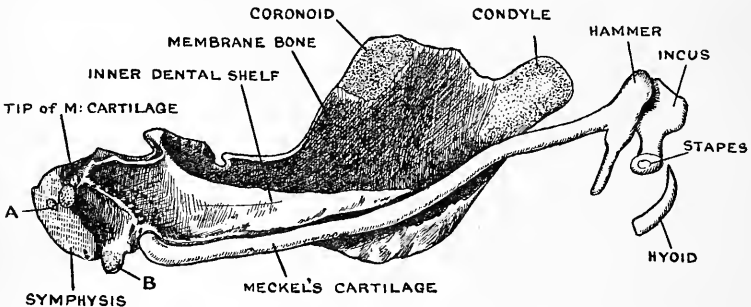


FIG. 178.—Meckel's Cartilage and Mandible of a Foetus in the 4th month of development, viewed on the inner or lingual aspect. (From a drawing and reconstruction by Dr. Alex. Low.) A and B, cartilaginous ossicles at symphysis; C, termination of Meckel's cartilage.

cartilage is the primitive skeleton of the mandible—a condition we know to occur in various forms of fishes (see Fig. 173). The malleus formed the upper end of the skeleton of the jaw, the joint between the malleus and incus representing the mandibular joint. The second stage in the evolution of the jaw is the formation of membrane or dermal bone to strengthen the cartilaginous rod and form supports for the teeth. This stage is also seen in fishes. The third and final stage is the formation of an ascending ramus and the evolution of a new joint between the condyle of the ascending ramus and the squamosal part of the temporal. This stage evidently occurred in the early ancestry of the mammals. In all other vertebrates—amphibians, reptiles and birds—the primitive joint persists.

Growth Changes in the Jaw.—The mandible undergoes great changes in the course of growth. As the permanent teeth erupt behind the milk set, increased alveolar space is required. This is obtained (see Fig. 179) by new bone being deposited along the posterior border of the ascending ramus, while absorption takes place at the anterior border. Growth in the vertical height is obtained by the deposition of new bone along the upper border of the ramus. Growth of the upper jaw and of the antrum

of Highmore, by pushing downwards the body of the lower jaw, leads to an elongation of the ascending ramus, and to its assuming a more vertical position to the body of the jaw (Fig. 179). In old age, when the teeth drop out and the alveolar margins are absorbed, the ascending ramus again becomes oblique, to allow the lower jaw to come in contact with the upper during mastication. The **mental eminence** is present at birth, and is a human characteristic. In apes the genioglossal muscles arise from a fossa, in place of a tubercle as in man, on the lingual aspect of the symphysis. In primitive races this simian fossa occasionally occurs.¹

As the teeth erupt, growth occurs both at the lower and alveolar borders, and also over the mental eminence or chin. These growth changes are well exemplified in the subjects of acromegaly (Fig. 179). In this disease growth

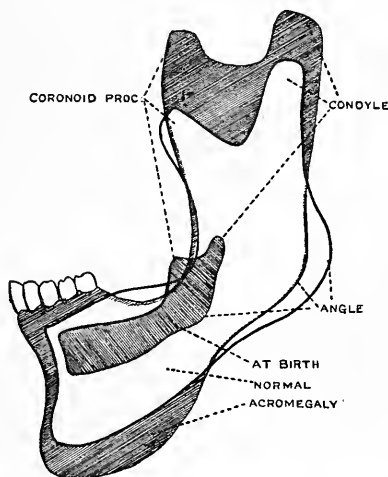


FIG. 179.—Mandibles of a Child at Birth, of a Normal Adult and of a Man, the subject of the disease of growth known as Acromegaly, superimposed to show the manner in which growth takes place.

of the jaw proceeds after adult years are reached. The deposition of new bone at the condylar process leads to the chin and teeth being pushed forwards in front of the upper jaw and teeth. The chin and lower border also increase in size.

The Temporo-mandibular Articulation.—Two types of this joint are found in mammals, one (see Fig. 180, *A*), exemplified in the carnivora, in which only a hinge action is permitted, and hence the jaws act like scissor blades; the second (see Fig. 180, *C*), in which a gliding movement is allowed, the teeth being thus able to act as grinders. The second type occurs in all vegetable feeders. The human articulation combines the characters of both types (Fig. 180, *B*), the gliding action taking place between the interarticular cartilage and the skull, the hinge action between the cartilage and the condyle. In rodents the glenoid cavity is a narrow

¹ For the morphology of chin and symphysis see Professor Arthur Thomson, *Journ. Anat.* 1916, vol. 50, p. 43.

gutter in which the plate-like condyloid process glides backwards and forwards. The interarticular cartilage is developed in all the Mammalia except the monotremes, and one or two marsupials (Parsons).¹ At the end of the third month the cartilage appears as a condensation of fibrous tissue between the coronoid process and root of the zygoma. There is at this time no articular cavity; the disc appears to arise from tissue caught between the condylar process and future glenoid cavity (Vinogradoff).

Development of the Tympanic Plate and Articular Eminence.—If the chin be depressed the condyle of the jaw moves on to the articular

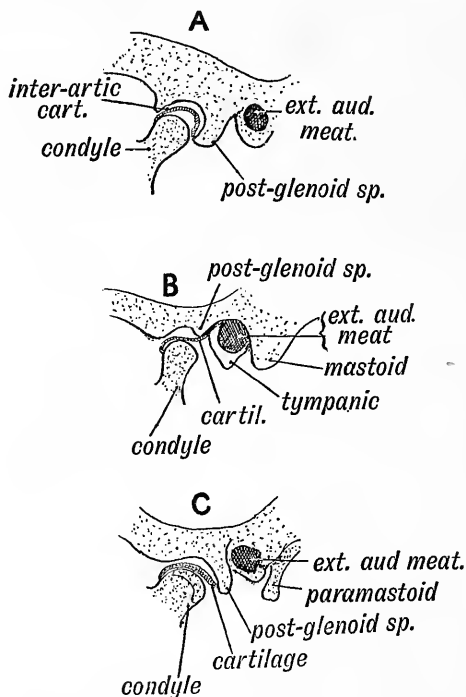


FIG. 180.—The chief types of the Temporo-Maxillary Articulation.
 A. Carnivorous Type. B. Omnivorous Type. C. Herbivorous Type.

eminence (Fig. 180, B); if over-depressed it springs over the eminence, and a dislocation is produced. This is impossible in the early years of life, for at birth there is no eminence and no glenoid cavity (see Fig. 181, A). At birth the **membrana tympani** lies exposed on the surface of the skull behind the condyle, supported in a fine osseous hoop, the **tympanic ring**. The ring is imperfect above, and there the flaccid part of the membrane occurs. By the second year the ring has grown into a plate by sending out two processes, which, as they grow out, unite and leave a gap between (Fig. 181, B). This, as a rule, is soon filled up. By the 20th year the tympanic plate is three-quarters of an inch long, forming the

¹ "Joints of Mammals," *Journ. of Anat. and Physiol.* 1900, vol 34, p. 41.

bony floor of the external meatus and the posterior wall of the glenoid fossa, which in man is remarkably deep. It protects the meatus from the condyle, and must be regarded as an accessory part of the mandibular joint. Every year until the 20th the bony meatus gets longer, while the fibro-cartilaginous part becomes relatively shorter. In the adult the bony part forms two-thirds of the meatus. As the tympanic plate grows

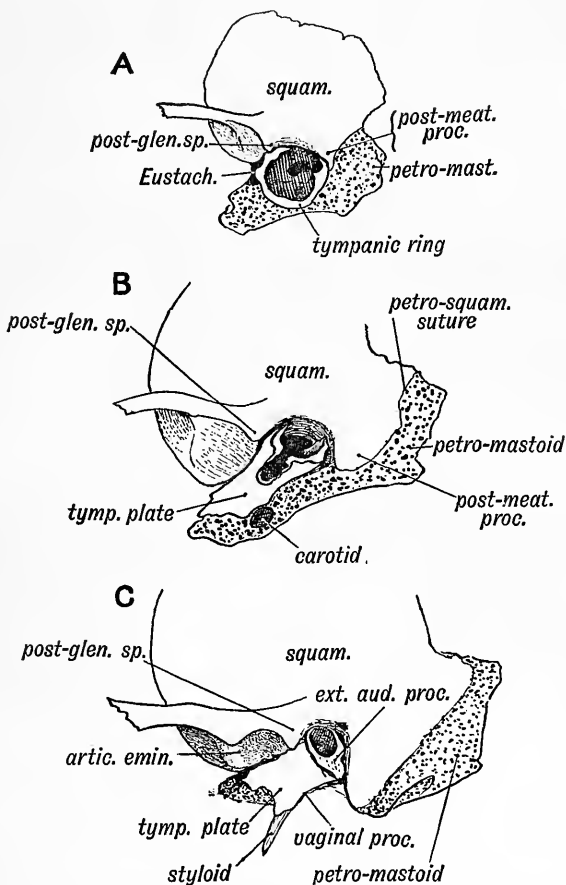


FIG. 181.—Showing the chief changes after birth in the form of the Temporo-Maxillary Articulation.

A. At Birth. B. At Two Years. C. In the Adult.

outwards, the membrana becomes less easily accessible to the surgeon (Fig. 181, C). The plate also grows inwards to form the floor of the bony part of the Eustachian tube and downwards to form the vaginal process, to which the upper end of the carotid sheath is attached (Fig. 181, C).

Fate of the Stomodaeum.—Having described the manner in which the three developmental masses—nasal, maxillary and mandibular—are involved in the upbuilding of each side of the face, it may be profitable

to look back and see what has become of the primitive oral cavity—the stomodaeum. A diagrammatic section of this cavity is given in Fig. 182; up to the 5th week it is separated from the primitive pharynx by the oral membrane; the pituitary evagination—Rathke's pocket—is seen arising

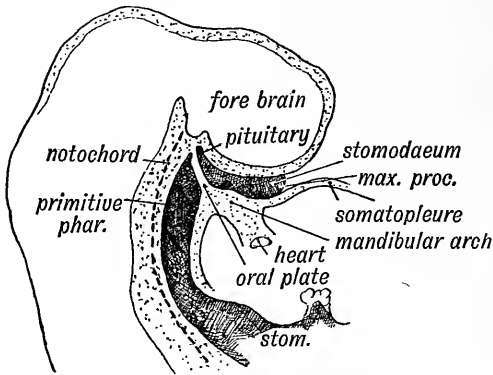


FIG. 182.—Sagittal Section showing the Stomodaeum and position of the Oral Plate in the 4th week. (Schematic.)

from the stomodaeum at the dorsal margin of the membrane. When the prechordal plate of cartilage is formed below the fore-brain, the *pituitary body* thus becoming an intracranial organ, its stalk comes to be situated at the hinder or sphenoid end of the nasal septum or vomer. This vomerine

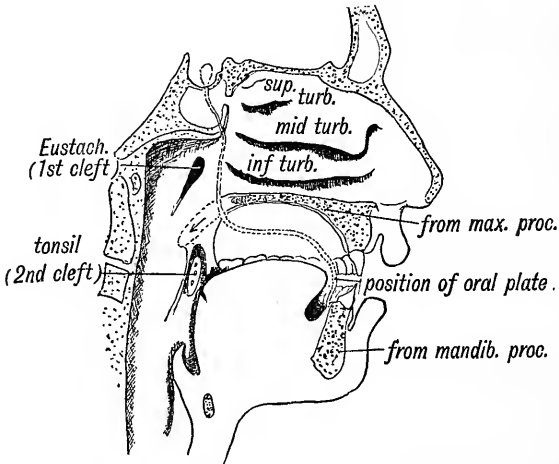


FIG. 183.—Showing the fate of the Stomodaeum. The relative position of the Oral Plate is indicated.

point may be regarded as stationary during the development of the nasal and buccal cavities. In Fig. 183 the position is shown which the oral plate would assume were it to persist until adult life. The lips and teeth are developed in front of it, and therefore within the cavity of the stomodaeum. The hard palate is developed in front of it but only part of the soft. The

nasal cavities are not derived from the stomodaeum. It is true that the nasal processes grow within and fill up the primitive space as it expands, but the cavities within the nasal processes represent expansions of the primary olfactory pockets. The tongue and floor of the mouth arise in the pharynx, behind the oral plate.

In this chapter an account has been given of the various embryological elements which go to form the face. In the chapters dealing with the eye, nose, teeth and tongue further details will be described. The chief feature of the human face is its power of expression—due to the high differentiation of its subcutaneous musculature, and to the elaborate nervous mechanism controlling that musculature. The muscles of expression, we shall see, arise in connection with the hyoid arch; their wide distribution on the face occurred with the evolution of the pulmonary respiratory system.

CHAPTER XIII.

THE TEETH AND APPARATUS OF MASTICATION.

IN previous chapters dealing with the Cranium and Face, many of the changes in the apparatus of mastication have already been mentioned. At the end of the second year the alveolar parts of the palate and mandible are only sufficiently large to carry the milk dentition—which comprises 20 teeth altogether, 8 of these being incisors, 8 milk molars, and 4 canines. During the eruption of the permanent teeth, from the 5th to the 22nd year, space has to be found for the 12 permanent molar teeth, the place of the milk teeth being occupied by the permanent incisors, canine and premolar teeth. Hence the rapid growth of jaws, the enlargement and strengthening of the face, the development of supra-orbital ridges and the upgrowth of the temporal line, which are seen to take place as the permanent teeth come into position. At the same time growth changes affect the muscles of mastication.

Evolution of Teeth.—The teeth are products of the skin. Both the cutis or dermis and the epithelium or epidermis enter into their formation. A tooth is a papilla of the dermis which has undergone a peculiar form of ossification (dentine); it is coated by an extremely hard substance—enamel—which is formed by the epidermis. Between the placoid scales which cover the skin of the shark and the complicated molar tooth of an elephant, there is a connecting series of intermediate forms. The primitive teeth have a conical or peg-like form, but with the evolution of mastication in the primitive mammalian stock the conical teeth became differentiated into various and complicated forms—the molar teeth departing very markedly from the primitive simple type. The recognition of the true nature of teeth was delayed by the fact that, during the development, the dental papilla and its epidermal covering are submerged beneath the lining membrane of the mouth.

The Structure of a Tooth.—A tooth may be considered as made up of five parts (see Fig. 184):

(1) The **pulp**, situated within (2) a capsule of **dentine**; the exposed part or crown of the dentine is coated by—(3) the **enamel**; the embedded part or root by a layer of bone—(4) the **crusta petrosa**. The root is secured within its socket by (5) the **peridental membrane**, which acts as a periosteum to both the crusta petrosa and bony wall of the tooth socket. An account of the development of a tooth has to deal with the origin of each of these five parts.

(1) **Origin of the Enamel.**—The enamel buds are formed by the ectoderm of the stomodaeum. In the 7th week the ectoderm within the labial margin grows within the underlying mesodermal tissues so that a narrow semicircular invagination of epithelium is formed within the mandibular arch below, and within the premaxillary and maxillary parts of the primitive palate above. To the plate of ectoderm thus infolded the name of **dental lamina** or **shelf** is given. As may be seen in a section of the foetal lower jaw (Fig. 185) the dental lamina is continuous at its origin with the epithelial downgrowth which separates the lip from the alveolus. From the ingrowing or deep margin of the dental lamina ten epithelial buds arise during the 3rd month, both in the upper and lower jaw. Each of these twenty **enamel buds** or **organs** produces the enamel to cover the crown of a milk tooth. Each bud as it deepens and expands comes against

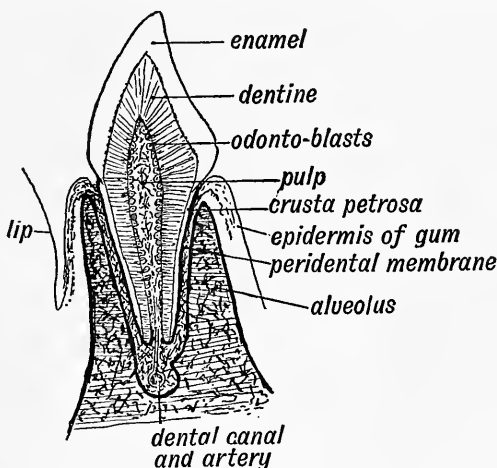


FIG. 184.—Showing the parts of an Incisor Tooth.

a condensed formation in the mesoderm of the jaw—the **dental papilla**.¹ On the papilla the enamel bud becomes partly invaginated, the mesodermal or odontoblastic bud coming to lie within the invagination (Fig. 185). During the 4th month the deeper stratum of ectodermal cells which cover the papilla change into columnar enamel-producing cells or **ameloblasts**. The basal part of the ameloblasts is converted gradually into enamel, or to put it somewhat differently, the ameloblasts form and deposit enamel in their bases and thus produce a coating for the dental papilla. Each ameloblast is gradually converted into an enamel fibre, their more superficial parts are never so converted, but persist as the **cuticular membrane** (Nasmyth's membrane) which covers the enamel at birth and is soon afterwards worn off. The enamel of the milk teeth is completely formed before birth; and that of the first permanent molar is already partly deposited. From the 5th month onwards the dental lamina—between the

¹ A. Masur, *Anat. Hefte*, 1907, vol. 35, p. 263 (Dev. of Dental Pulp); J. Howard Mummery, *The Microscopic Anatomy of the Teeth*, 1920.

tooth germs and the surface of the alveolar margin—undergoes a gradual disruption and absorption. Isolated masses of the lamina may persist within the gums and in certain cases give rise to masses of dental tissue—odontomes.

(2) **Origin of the Dentine.**—The dental papilla or odontoblastic germ, formed from the mesoderm, corresponds to a depressed skin (dermal) papilla, the enamel cells representing its covering of epithelium. The dental papilla determines the shape of the tooth. In its superficial layers it contains numerous cells, **odontoblasts**, with branched processes radiating towards the enamel epithelium. By the agency of the odontoblasts a substance is deposited which becomes calcified into dentine or ivory. It is deposited in the matrix round the processes of the odontoblasts. The cavities in which the processes are enclosed form the tubules of the dentine. In rodents especially, but also in all mammals, although only to a slight

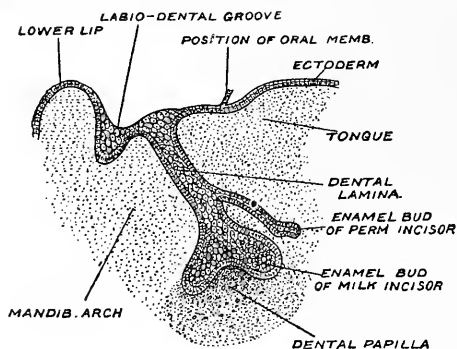


FIG. 185.—Section through the Lip and Mandible of a Foetus in the third month of development, showing the down-growth of the Dental Shelf.

extent in civilized races of mankind, the odontoblasts react to wear, add new layers of dentine to the wall of the pulp cavity, and thus prevent the pulp from being exposed. The dentine is deposited first in the crown of the tooth beneath the enamel; the neck is laid down next, and then the root, the last point of all to be formed being the narrow canal at the apex of the root by which the dental vessels and nerves reach the pulp cavity. The dental crowns reach their full size at the time of their formation. Teeth thus differ from all other structures of the body in undergoing no growth subsequent to the period of their development.

(3) **The Pulp.**—The pulp represents the remnant of the odontoblastic germ enclosed by the dentine. It is made up of a matrix of branching cells and contains the ramifications of the artery, vein and nerve of the tooth. Fine processes of the nerves pass into the dental tubules, while in its peripheral zone are situated cells possessing the characteristics of nerve cells (Mummery).

(4) **The Dental Sac.**—The foetal tooth, as may be seen from Fig. 186, lies embedded in the alveolus surrounded by a fibrous capsule known as the dental sac. The sac and its contents form a **dental follicle**. When the

enamel bud is invaginated by the dental papilla, the **invaginated** wall forms the enamel-producing layer, while the **invaginating** or parietal wall becomes surrounded by a dense layer of mesodermal tissue. The parietal wall is converted into the dental sac. At first (Fig. 185) the dental sac is continuous with the odontoblastic germ; it becomes separated from the pulp when the root or roots of the teeth are completed. Between the enamel (invaginated) and parietal (invaginating) layers, filling the cavity of the sac, lies a mass of jelly-like epithelium corresponding to the corneous epithelium of the skin. As the crown of the tooth grows it rises within the sac of the enamel germ, and causes the absorption of the gelatinous material (Fig. 187).

(5) **The Peridontal Membrane.**—The peridontal membrane (Fig. 184) is formed by that part of the dental sac which surrounds the fang of the

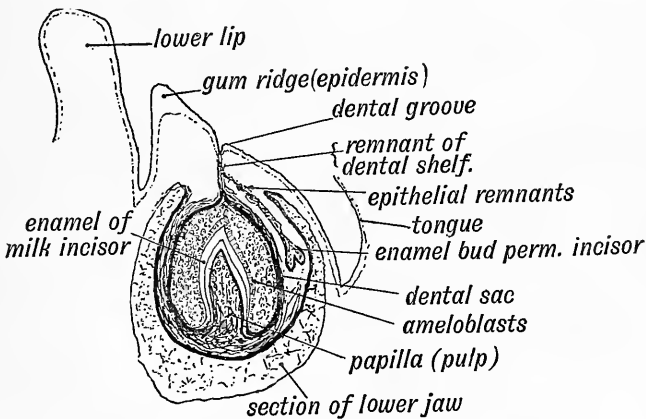


FIG. 186.—Showing the stage of development in an Incisor Tooth of a Foetus of six months.

tooth. The part of the dental sac which surrounds the crown is absorbed during the eruption of the tooth.

(6) **The Crusta Petrosa.**—The peridontal membrane is of the nature of periosteum, and contains osteoblasts which deposit the crusta petrosa (bone) on that part of the dentine which forms the fang and also on the inner wall of the alveolus. The centres of ossification in the upper and lower jaw spread round the labial and lingual aspects of the dental sacs, thus enclosing them in a bony gutter or trough. Subsequently septa are developed between the dental sacs, and thus the developing teeth come to be situated in bony crypts. The roof of a crypt is never completed; a hole or window persists through which the neck of the dental sac emerges to become continuous with the mucous membrane covering the alveolus. The crowns of the teeth erupt at the point of union between the dental sac and alveolar membrane.

Epithelial Remnants of Enamel Organ.—Epithelial remnants of the dental lamina are to be found in the substance of the alveolus up to the end of foetal life or later, and may give rise to cysts of various kinds.

Besides these there are also others which occur within the sac surrounding an uncut tooth, representing remains of the enamel organ. In Fig. 187 is depicted a section of an unerupted first permanent molar tooth, lying within its dental sac, remnants of the enamel organ being shown distributed within the sac from the crown to the growing ends of the roots. We have seen that the enamel organ represents an epithelial sac, only the inner or invaginated wall being concerned in the formation of the enamel, the outer or enveloping layer becoming broken up as shown in Mr. Mummery's figure,¹ to form an interrupted epithelial layer sometimes named Hertwig's sheath.

Origin of the Permanent Teeth.—From the dental shelf, besides the buds for the milk teeth, there grow inwards, during the latter part of the

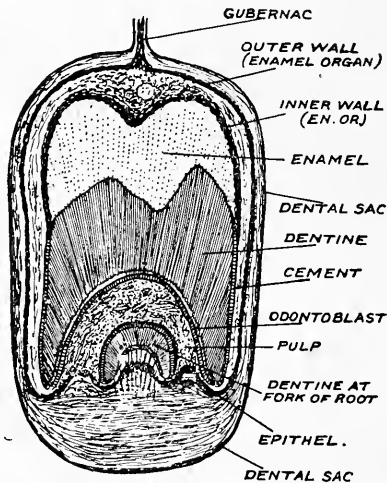


FIG. 187.—Epithelial remnants in the Dental Sac of a first Permanent Human Molar. (Howard Mummery.)

3rd month of development, so as to lie on the lingual aspect of the milk buds, processes of ectoderm which form the enamel of the ten teeth which replace the milk teeth (Figs. 185, 156 and 158). The three permanent molars of each side arise from a process which prolongs the dental lamina backwards behind the part from which the enamel buds of the milk teeth arise (Fig. 188). The first molar is the earliest of all the permanent teeth to undergo development. The permanent teeth are formed in exactly the same manner as the milk set. They develop on the lingual aspect of the roots of the milk teeth (Fig. 186), and if the milk teeth be roughly extracted the permanent bud may also be torn out. Being developed deeper in the alveolus than the milk teeth, the neck of the dental sac is more elongated, and has been named the **gubernaculum dentis** under the belief that it serves to guide the teeth during eruption. The opening by which the gubernaculum emerges from the crypts of the permanent incisors and canines is

¹ J. Howard Mummery, *Phil. Trans.* 1919, vol. 209 (B), p. 305.

seen on the lingual side of the alveolus near the sockets of the corresponding milk teeth. In the case of the premolars, the openings lie within the crypts of the milk molars (Carter).

Dentigerous and other Cysts of the Jaw.¹—Cysts with epithelial walls, containing fluid, teeth or other dermal contents, occasionally develop in the jaw. They are formed from epithelial remnants of the dental lamina,

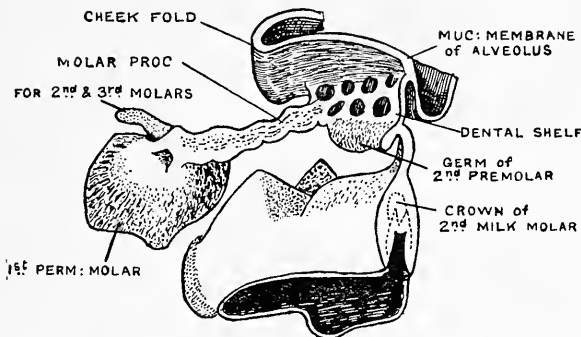


FIG. 188.—Mucous Membrane covering the posterior part of the Alveolus of a newly born Child with the Dental Shelf still attached to it. Proceeding backwards from the end of the dental shelf is seen the "molar process," which gives rise to the three permanent molar teeth. The crown of the second milk molar and the germ of the second premolar are also shown. (After Röse.)

which normally breaks up and disappears completely, or from detached parts of the enamel buds.

Number of Dentitions.—In many lower vertebrates, such as sharks, the dental lamina gives off constantly a series of buds, so that as soon as one tooth is lost another springs up in its place from behind (Fig. 189). In mammals generally, as in man, the dental lamina gives off only two series of

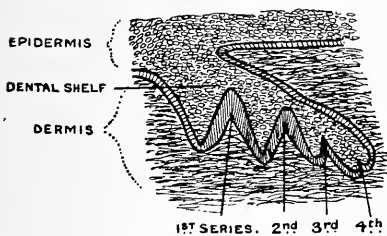


FIG. 189.—Diagrammatic Section across Dental Shelf of a Shark showing a Succession of Dentitions. (After Vialleton.)

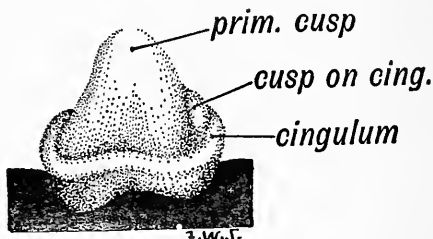


FIG. 190.—Premolar Tooth of a Carnivorous Mammal to show the Primitive Cone, Cingulum and Secondary Cusps springing from the Cingulum. (Marett Tims.)

buds—one for the milk set and another for the permanent set. In marsupials it gives off only one series, so that the first set of teeth is never replaced by a second. Thus in the most primitive vertebrates there is a succession of teeth, owing to the fecundity of the dental shelf. In man there are only the primary and secondary broods, but it is possible that

¹ P. Adloff, *Anat. Anz.* 1912, vol. 40, p. 177 (Abortive Dental Buds).

occasionally representatives of a 3rd brood may be produced, for there are cases on record where a permanent tooth has been replaced by another late in life.

Morphology of Human Teeth.¹—The crowns of all the human teeth seem to be modifications of the same type, all being evolved from the simple conical tooth found in fishes and reptiles (Figs. 190, 191). The conical peg-like tooth is to be regarded as the most primitive type, and in man vestigial teeth of this type occasionally occur. A modified example of the type is seen in the premolars of carnivorous mammals (Fig. 190). Here the base of the peg-shaped crown is surrounded by a ring of enamel—the **cingulum**. From the conical tooth was evolved the **tritubercular** type, one in which the crown carries three tubercles or cusps, two on the labial side of the crown and one on the lingual margin (Fig. 191, *A*). Secondary cusps arise from the cingulum (Marett Tims), and by the fusion of these with the original cone the two outer cusps are produced, while

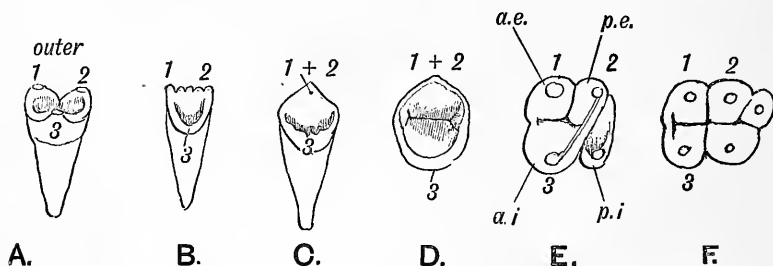


FIG. 191.—*A*. The Tritubercular Type of Tooth. The corresponding cusps are shown in the crowns of an Incisor (*B*), Canine (*C*), Bicuspid (*D*), Upper Molar (*E*), and a Lower Molar (*F*).

the inner cusp arises within the cingulum. The canine retains the conical form of crown; the prominence or heel on the lingual aspect of the crown represents the inner cusp; occasionally this cusp is well developed on the human canine (Farmer). The cutting edge of the incisors represents the two outer cusps; when newly cut, the incisor crowns show five serrations or cuspules. In the premolars or bicuspids the outer cusp, as may be seen in many of the lower primates, is really double.

In the upper molar teeth, to the three primary cusps which form a cup, a fourth has been added (see Fig. 191, *E*). The two outer or buccal cusps are distinguished as the A.E. cusp (antero-external), the P.E. cusp (postero-external); the two inner as the A.I. (antero-internal) and P.I. (postero-internal). In the upper molars the cusps are situated alternately and the P.E. and A.I. cusps are united by an oblique enamel ridge, which represents the posterior margin of the crown of the primitive tritubercular tooth (Fig. 191, *E*). In the upper molar teeth of civilized races, especially in their wisdom teeth, the 4th or posterior internal cusp is often absent, the

¹ A. C. F. Eternod, *Verhand. Anat. Gesellsch.* 1911, p. 144 (Bicuspid Theory of Teeth); Sir C. S. Tomes, *Manual of Dental Anatomy*; Prof. L. Bolck, *Versuch. einer Lösung der Gebissprobleme*, Jena, 1913; *Amer. Journ. Anat.* 1916, vol. 19, p. 91; *Journ. Anat.* 1921, vol. 55, p. 138; T. Wingate Todd, *Introduction to Mammalian Dentition*, 1918; D. M. Shaw on use of dental cusps, *Journ. Anat.* 1918, vol. 52, p. 97.

primitive tritubercular tooth thus reappearing. In the lower molars two cusps have been added to the three primary ones, making five in all. The fifth cusp is situated at the posterior border of the crown; the others are arranged in opposite pairs. The fifth cusp has become lost in the 2nd and 3rd lower molars of civilized races. Harrison found in *Sphenodon*, a primitive type of lizard, that **concrecence** or fusion of the simple peg-like teeth takes place in the posterior part of the jaw; it is possible that the molar teeth of mammals may have originated thus (Marett Tims). **Gemination** may occur in human incisors; the incisor bud divides so that two crowns are produced on one root.¹

The Roots.—The upper molar teeth have three roots, two outer and one inner, but in the wisdom teeth, especially of civilized races, the roots are usually fused. The lower molars have two roots, but each root appears to be essentially double in nature. In lower primates the upper bicuspids have three roots, but in man these are usually fused so as to form one or sometimes two roots. The lower bicuspids have usually one root, but as in lower apes, they may have two. The roots are the last parts to be formed. When the roots of the molar teeth come to be developed, the base of the dental papilla is differentiated into three parts—round each of which a root is formed (Fig. 187). In that peculiar ancient and extinct race of men—known as the Neanderthal race—the dental papilla and pulp cavity were very large and the roots were short and wide. Thus in **Neanderthal teeth**—the condition is occasionally seen in a modern tooth—the pulp cavity almost descended to the tips of the roots.²

Eruption of the Teeth.³—The eruption of the milk teeth commonly covers a period of eighteen months, beginning in the 6th with the lower incisors and ending in the 24th or 30th with the 2nd milk molars. The eruption of the permanent teeth occupies a period of about eighteen years, beginning with the 1st permanent molar in the 6th year and ending about the 24th with the 3rd molar. The milk molars are replaced by the permanent premolars. In civilized races the third molars or wisdom teeth frequently remain embedded in the alveolus or may be quite absent. The upper wisdom tooth is developed in the posterior border of the superior maxilla, which bounds the speno-maxillary fissure in front. In growth backwards of the maxillary antrum the posterior border of the superior maxilla becomes rotated into the alveolar border, thus bringing the wisdom teeth into position (see Fig. 176). The inferior wisdom teeth are developed in the alveolus on the inner aspect of the ascending ramus.

A fourth molar sometimes appears behind the third. The original primate stock is supposed to have had three incisors and four premolars on each side, yet a supernumerary incisor or premolar is a rare abnormality. The upper lateral incisor may be very small or even absent, there being a distinct tendency towards the disappearance of this tooth

¹ J. T. Wilson and J. P. Hill, *Quart. Journ. Mic. Sc.* 1907, vol. 51, p. 137 (Tooth Formation in Monotremes); W. Ramsay Smith, *Journ. Anat. and Physiol.* 1907, vol. 42, pp. 126, 226 (Morphology of Teeth of Australian Natives).

² Keith and Knowles, *Journ. Anat. and Physiol.* 1911, vol. 46, p. 12.

³ G. Fischer, *Anat. Hefte*, 1909, vol. 38, p. 617 (Eruption of Permanent Teeth).

in civilized races. If the teeth are too large for the jaw, a not uncommon condition in civilized races owing to a diminished growth of the bony palate, they appear in irregular positions.

Mechanism of Eruption.—As regards the mechanism which causes teeth to erupt there is still some degree of uncertainty. One naturally infers that the growth of the root will tend to force the crown upwards and the tissues over the crown to atrophy. The process of eruption is a much more complex one than the mere formation of a root. It is well known that a rootless tooth may cut the gum, while in another case the root may form and yet the tooth remain embedded in the jaw. Eruption is a definite growth movement—allied in nature to the mechanism which leads to the extrusion of a foreign body by the tissues. During the eruption of a tooth there is not only an absorption of the overlying tissues of the gum—probably due to pressure—but there is also the positive growth of the peridental tissues at the base of the tooth-sac which, as it presses the tooth towards the surface, moulds the surrounding wall of the dental crypt into a suitable alveolar socket. Thus the formation of the socket or alveolus appears to be part of the mechanism of eruption. Mr. J. T. Carter regards the gubernaculum dentis as playing an effective part in tooth eruption.¹

Effect of Civilization.—Mention has been made of the fact that the eruption of the last molars in highly civilized peoples may be long delayed or arrested; in a small proportion of individuals these teeth may be quite absent. When the teeth and jaws of ancient European races are compared with those of their successors, certain changes are very evident. These are (1) the crowns of the teeth in the ancient races are much worn; (2) the palate is well formed, and large enough to carry the teeth without crowding or irregularity; (3) the wisdom teeth are in position, but usually show a reduction in size and development; (4) diseased and carious teeth are uncommon; (5) the edges of the incisor teeth come into apposition in biting. In modern Europeans the degree of wear or erosion is slight; the palate is often vaulted, contracted and the teeth crowded and misplaced; the wisdom teeth are often unerupted or absent; diseased teeth are extremely common; the edges of the lower incisors ascend behind the crowns of the upper (scissors bite). The cause or causes of these remarkable changes are ill-understood, but it is probable that some or all will be traced to the nature of our modern dietary.

Muscles of Mastication.²—The four muscles of mastication—the temporal, masseter, external and internal pterygoids arise in the mandibular arch. A single muscular mass is apparent at the end of the first month; during the second month it is differentiated into its several parts—the internal pterygoid being the first to separate from the common mass. The masseter and external pterygoids are derived from the primitive temporal muscle. The external pterygoid is a late addition; even in man it is often imperfectly separated from the temporal. The muscles of

¹ See *Brit. Dent. Journ.* 1904, Feb.

² Professor F. H. Edgeworth, *Quart. Journ. Mic. Sc.* 1914, vol. 59, p. 573.

mastication differ from the ordinary striated muscles of the body in being derived from the musculature of a visceral arch. Their motor nerve—the motor root of the Vth—represents the splanchnic nerve of the second segment of the head (see p. 99). The somatic motor nerve of the segment is the 4th or trochlear nerve; the somatic musculature of this segment is represented by the superior oblique. The sensory nerves of the teeth—the 2nd and 3rd divisions of the Vth nerve—represent the skin or somatic sensory fibres of the second or mandibular segment of the head. It will be thus seen that the apparatus of mastication has been evolved in connection with the second cephalic segment—the neuromere of this segment being the second of the mid-brain. The manner in which the muscles of mastication are attached to the skull, and the extent to which they modify cranial characters have been already mentioned (p. 155). The evolution of the temporo-mandibular joint has also been alluded to (p. 177).

CHAPTER XIV.

THE NASAL CAVITIES AND OLFACTORY STRUCTURES.

Evolution of the Nasal Cavities.—Although the sense of smell is a minor one in the economy of the human body, it is very evident that in the root-stock from which mammals have been evolved the olfactory organ must have held a foremost place amongst the sensory structures. We have seen that the great superstructure of the brain rests on the primary ganglia connected with the olfactory nerves. When now we examine the changes connected with the development of the nose and nasal cavities in

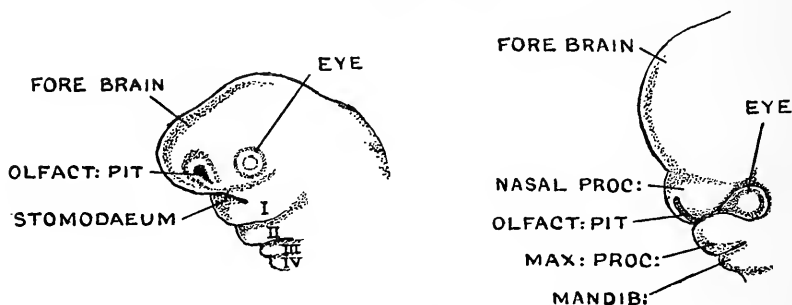


FIG. 192, A.—The Olfactory Pit and Face of an Embryo in the 5th week of development. (After Broman.)

FIG. 192, B.—The Olfactory Pit and Facial Processes in an Embryo in the 6th week of development. (After Hochstetter.)

the human embryo, we shall see, behind the complicated processes at work, a recapitulation of conditions which are to be seen in animals occupying a very low position in the vertebrate kingdom. At the end of the 4th week the olfactory membrane appears as two plaques of ectoderm in contact with the under surface of the fore-brain (Figs. 155, A, 192, A); in the 5th week the plaques or plates become two pits—right and left, the usual condition in fishes; in the 6th week each pit becomes connected with the primitive mouth or stomodaeum by a groove—a condition seen in the dog-fish; in the 6th and 7th weeks the pit is deepened and its opening becomes turned towards the stomodaeum owing to the growth of its lateral and mesial margins which form the lateral and mesial nasal processes (Fig. 155). The processes unite in the manner already described and a nasal cavity similar to that of the air-breathing or dipnoan fishes is established. In the 7th and 8th weeks the cavity of the pit is rapidly enlarged;

free communication with the mouth is established ; the nasal cavity has then become, as in amphibians, the functional vestibule of the respiratory system. In the 3rd month the palate is complete, and the stage peculiar to mammals thus established.

In tracing the development of structures subservient to the sense of smell, the following elements have to be dealt with :

- (1) The olfactory sense epithelium and olfactory nerves ;
- (2) The parts of the brain concerned with the sense of smell ;
- (3) The capsule which contains the olfactory epithelium ;
- (4) The respiratory tract of the nasal cavities.

(1) **Origin of the Olfactory Sense Epithelium.**¹—At the end of the 4th week, a small area of the ectoderm lying under the fore-brain becomes demarcated on each side, to form the **olfactory plates**. Around these two plates the lateral and mesial nasal processes grow up (Fig. 193), the plates

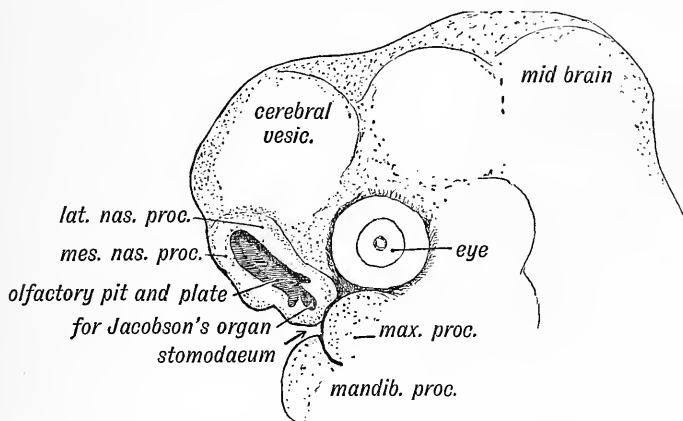


FIG. 193.—The Olfactory Pit and Nasal Processes in a Human Embryo about 5 weeks old. (After Kollmann.)

becoming at the same time invaginated to form the **olfactory pits**. With the growth of the nasal processes the cavities of the expanding olfactory pits or pockets come to occupy a space on the roof of the stomodaeum, their openings being turned towards that cavity. The ectodermal lining becomes the epithelial membrane of the nasal cavities. A small island is detached from each olfactory plate to form the basis of Jacobson's organ (Fig. 193). The sense epithelia in the olfactory area behave as nerve cells and send out nerve processes which form arborescences round the neural cells of the outgrowing olfactory bulb (Fig. 194). The olfactory nerves are thus formed. At first the olfactory plates are directly in contact with the cerebral vesicle, but later on they are separated by the formation of the cerebral membranes and cribriform plates.

In the foetus the olfactory or sense epithelium is relatively extensive, as is the case in mammals with a keen sense of smell. It descends almost

¹ For development of Nasal Cavities see J. E. Frazer, *Journ. Anat. and Physiol.* 1912, vol. 46, p. 416 ; K. Peter, *Ergebnisse der Anat.* 1911, vol. 20, p. 43.

to the lower border of the middle turbinate on the outer or lateral wall, and to the junction of the upper two-thirds with the lower third on the mesial or septal wall. In the adult the distribution is much restricted—occupying areas only about one finger breadth in extent below the cribriform plate.

(2) **The Olfactory Lobe.**—As the olfactory pits are being thrust into the roof of the stomodaeum during the 6th week, the anterior part of the floor of the cerebral vesicles are growing out as hollow protrusions to form the olfactory vesicles. At the end of the 3rd month the olfactory vesicle has assumed the form shown in Fig. 194. Its cavity is at first continuous with that of the cerebral vesicle, but this connection is lost in the 3rd month; it becomes solid, and forms the olfactory bulb and tract (Fig. 196).

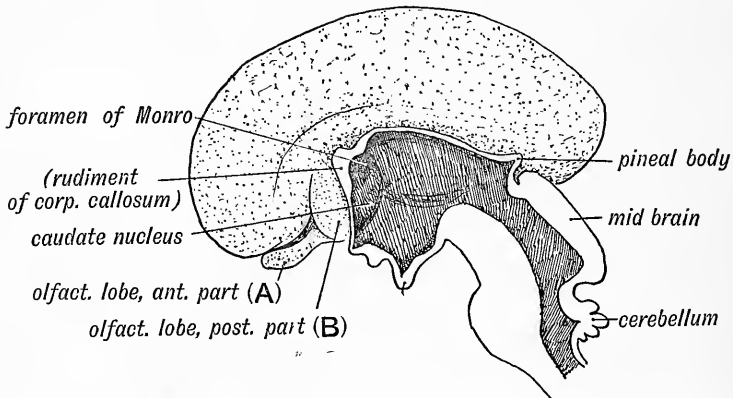


FIG. 194.—The Mesial Aspect of the Brain of a Human Foetus, 3½ months old, showing the Olfactory Lobe. *A*, olfactory bulb; *B* represents the paraterminal part of the rhinencephalon.

The tip of the anterior horn of the lateral ventricle marks the point at which the cavity of the olfactory lobe communicated with the cerebral vesicle.

The Rhinencephalon.—The Rhinencephalon is made up of the parts of the cerebrum which are primarily connected with smell. These parts are best seen in a typical mammalian brain such as is shown in Fig. 195. They are, following the classification of Elliot Smith: (1) the olfactory bulb and peduncle or tract, both of which are developed from the olfactory lobe; (2) the olfactory tubercle, represented in the human brain by a small area behind the trigone; (3) the paraterminal body (Figs. 194, 195) which is represented in the human brain by the gyrus subcallosus and septum lucidum; (4) the hippocampal formation represented in the human brain by the supra-callosal gyrus, gyrus dentatus, hippocampus and fornix (Fig. 196); (5) the pyriform lobe (the uncus of the human brain); (6) the anterior perforated space. In man these parts are reduced in size owing to (1) his less acute sense of smell; (2) the great development of the corpus callosum and mantle of the brain. The rhinencephalon represents the oldest part of the brain, and its grey matter differs from the rest of the cortex in structure.

Morphology of the Olfactory Neural Elements.—If the olfactory area of ectoderm were to adhere to, and form part of, the olfactory bulb, then the olfactory vesicle would be comparable to the optic vesicle, the rods and cones representing the olfactory epithelium, the ganglion cells of the olfactory bulb those of the retina, while the lateral and mesial olfactory tracts would correspond to the optic tracts. This homology is impaired by the fact that the fibres of the lateral olfactory tract end, not in a ganglionic mass, but in true cortex—that of the pyriform lobe or uncus (Fig. 195). The pyriform cortex is linked up with the gyrus dentatus by a second relay of fibres, while the dentate gyrus is connected in turn with the hippocampal cortex by a third relay. The fornix and the hippocampal commissure (see p. 122) represent the association and commissural system

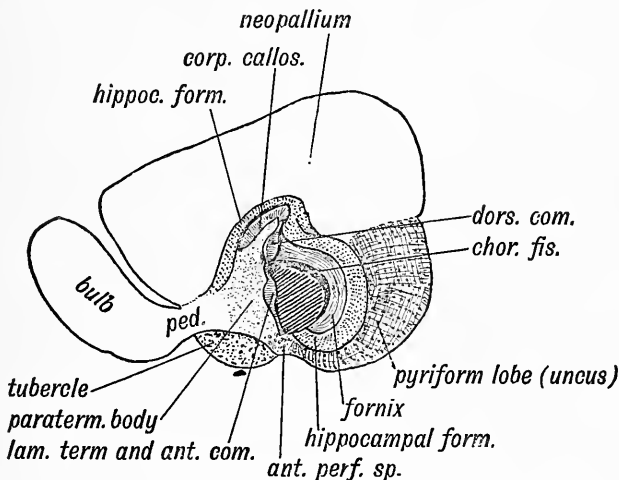


Fig. 195.—The Mesial Aspect of a typical Mammalian Cerebrum showing the parts of the Rhinencephalon. (Elliot Smith.)

of the hippocampal formation. The anterior commissure was originally made up of fibres passing from one olfactory bulb to the other (p. 121). Fibres in the mesial root of the olfactory tract reach the dentate gyrus by means of the fornix and supra-callosal striae.

The Nasal Cavities.—The nasal cavities are formed by the expansion of the olfactory pockets within the substance of the three developmental masses which surround each of them—the mesial nasal, lateral nasal and maxillary processes. When these processes unite in the 7th week, the primitive nasal cavity rapidly expands, and an opening temporarily closed is reformed in its fundus or floor, the primitive choanae, situated in the roof of the mouth (Fig. 170). The choanae are separated by the primitive nasal septum, and are at first in front of the pituitary outgrowth—Rathke's pocket (Fig. 197). In the latter part of the 2nd month and the earlier half of the 3rd the primitive nasal septum and the choanae on each side of it, extend their dimensions, until the posterior border of the septum reaches and involves the mouth of Rathke's pocket (J. E. Frazer). In this manner

the nasal septum is secondarily extended, and the nasal cavities greatly deepened (Fig. 197). At the same time the floor of the nasal cavities is prolonged backwards by the formation of the secondary palate, and the secondary choanae are established within the region of the naso-pharynx before the end of the 3rd month. The process of chondrification begins in the lower part of the lateral nasal process during the period at which the secondary palate is being formed. The chondrification of the lateral mass of the ethmoid and other parts of the olfactory capsule have already been described (p. 149).

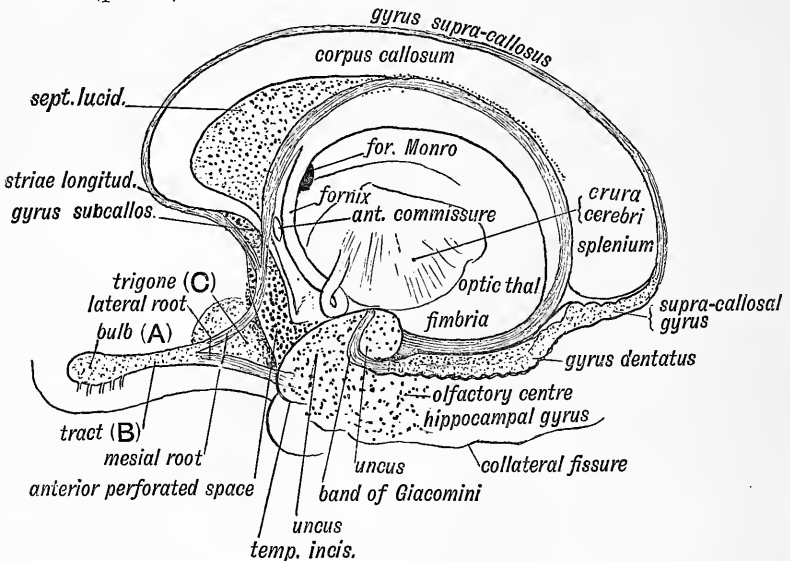


FIG. 196.—The parts of the Rhinencephalon in the Human Brain.

Development of Turbinates and Air Sinuses.¹—Before cartilage has actually been formed in the walls of the primitive nasal cavities, linear outgrowths of the lining epithelium are observed to occur in the lateral wall and roof. These outgrowths give rise to the meatuses of the nose—the inferior under the maxillo-turbinal appearing first, about the 8th week, the superior last, about the 12th week. In the lateral wall of the nasal cavity of a foetus 20 mm. long and in the 8th week of development Dr. Milne Dickie² found only two linear depressions—the lower representing the inferior meatus, the upper the *hiatus semilunaris* (ethmoidal infundibulum, Fig. 198). The turbinate processes are thus carved out of the lateral wall and roof of the nasal cavity. The usual number is five in mammals, but in man the 4th and 5th are only temporary. The *inferior or maxillo-turbinate* is developed on the lateral wall, but the middle and upper appear on the roof and septal wall, their lateral position being attained in the course of development. The sphenoidal turbinate also belongs to the ethmoidal

¹ See references, p. 174.

² *Journ. Anat.* 1914, vol. 48, p. 445.

series, but becomes applied to the body of the presphenoid. The turbinates and meatuses are developed in connection with respiration. They increase, it is true, the olfactory area, but their chief use is apparently to filter and warm the inspired air.

The manner in which the nasal mucous membrane pushes its way from the middle meatus into the maxillary process to form the **antrum of Highmore** has been already described (p. 173). The other air sinuses—the frontal, lachrymo-ethmoidal, anterior, middle and posterior ethmoidal, and sphenoidal sinuses—six in all, arise in the same way as the antrum, but begin, with the exception of the last named, to enlarge at a much later date. Although they begin to bud out about the time of birth, they assume their active growth in the earlier years of puberty, and reach their full size before the 30th year.

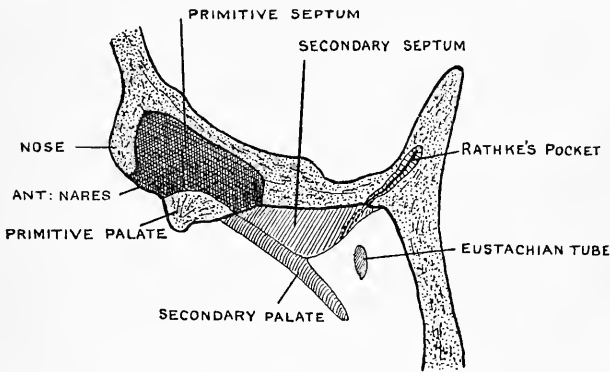


FIG. 197.—The Primitive Nasal Cavities and Choanae at the end of the 6th week. The formation of the secondary septum and palate are indicated. (After J. E. Frazer.)

At birth, the lateral mass of the ethmoid is a thin plate, carrying the superior and middle turbinate processes, which almost fill the nasal cavity (Figs. 169, 198). The entire ethmoid is narrow, and hence the proximity of the eyes in children. Beneath the middle turbinate is a thumbnail-like impression—the **hiatus semilunaris**, or ethmoidal infundibulum, one of the earliest formations (8th week). The maxillary sinus buds out near its posterior end, the point at which the bud arises becoming the site at which the sinus opens in the middle meatus (Fig. 199). The uncinatè process of the lateral mass of the ethmoid forms the prominent lower margin of the hiatus (Fig. 198). A second opening may be present below the level of the uncinatè process, or this may be the only one developed.

In Fig. 198 part of the middle turbinate has been removed to expose the *frontal recess* of the middle meatus—an expansion of the meatus formed in the 4th month of foetal life. At birth¹ four furrows are present—representing the buds of air sinuses. One, or occasionally two, of these

¹ I have followed the account given by Professor J. Parsons Schaeffer, *Amer. Journ. Anat.* 1916, vol. 20, p. 125.

enlarge to form the frontal sinuses, the others becoming cells of the ethmoid. The duct or mouth of the frontal sinus may become secondarily continuous with the hiatus semilunaris or the bud of the frontal sinus may arise from the upper end of the hiatus. The bud of the frontal sinus, as it expands, pushes its way into the frontal bone, separating the outer from the inner lamella. The bud is formed in the first year, but is nascent until the fifth. A second frontal bud may arise and partially or completely supplant the primary frontal outgrowth. As a rule, by the 25th year the sinus reaches outwards over the inner two-thirds of the orbital roof, and is an inch or more both in height and depth at its mesial part. It is smaller in women than in men, but it may be, and often is, arrested at an early stage of development, or it may be absent altogether. The size of the glabellar prominence is no index to its development.

The stalk of the frontal bud forms the infundibulum or naso-frontal duct, which is narrow, half an inch long, and difficult of catheterization

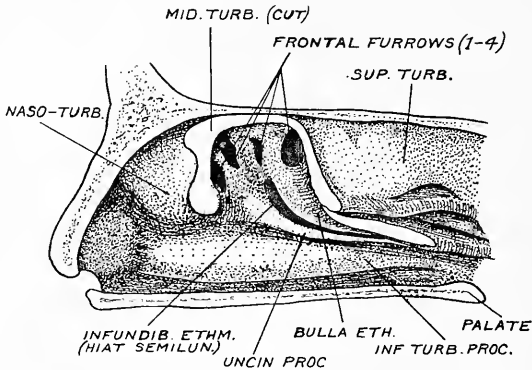


FIG. 198.—The Lateral Wall of the Nasal Cavity of a child at birth. (J. Parsons Schaeffer.)

from the nose. Into it open (or sometimes into the hiatus) the **lachrymo-ethmoidal** and **anterior ethmoidal cells** which surround the infundibulum. They are developed as outgrowths from the infundibulum (Fig. 199). Occasionally the maxillary sinus, as is frequently the case in the gorilla, sends a process to form part of the frontal sinus, and hence there may be a communication between the sinus and the antrum.

The development of the frontal sinuses and supra-orbital ridges leads to a marked change in the face at puberty. By the formation of the frontal sinuses the basal area of the skull, to which the face is attached, is largely increased in extent. Such an increase is necessary to support the palate, which grows rapidly in size at puberty. Up to the fifth year the upper jaw has to carry only ten milk teeth; in the adult it has to carry sixteen permanent teeth. To support these the face and palate have to be enlarged. The formation of the frontal sinus gives the necessary increase in the area of the base of the skull for their support. It should be remembered that the growth of the brain and of the cranial cavity is comparatively slight after the fifth year. Only the gorilla and chimpanzee

show an arrangement of frontal and ethmoidal sinuses comparable to that of man.

Above the hiatus lies the **bullae ethmoidalis**, which is inflated by, and commonly carries the opening of, the middle ethmoidal cell (Fig. 199). The posterior ethmoidal sinus opens beneath the superior turbinate process, and is developed from the superior meatus. The **ethmoidal sinuses** are produced in the cartilage of the ethmoidal or lateral nasal plate (Fig. 175). They inflate the ossifying cartilaginous plate until it becomes a cellular mass, thus increasing the breadth of the intra-orbital septum. The **sphenoidal sinus** (Fig. 199) is formed during the 3rd month by the mucous membrane growing into and expanding the sphenoidal turbinate bone, which is a small, slightly ossified cartilage lying beneath the presphenoid at birth, and forming the uppermost (sixth) of the nasal turbinate processes.

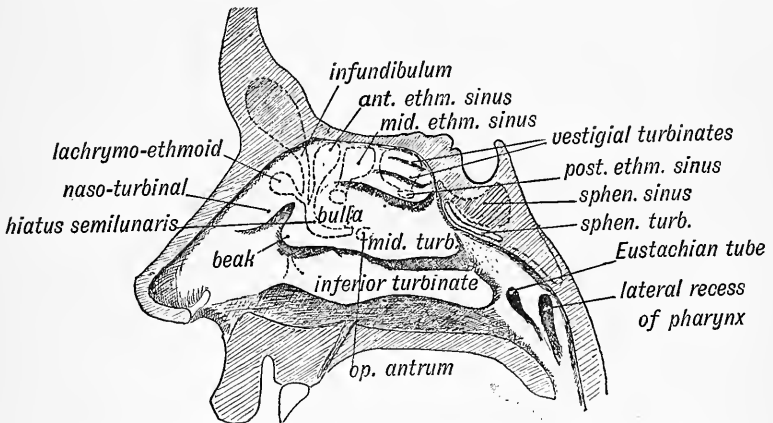


FIG. 199.—A Diagram of the Lateral Wall of the Nasal Cavity, showing the position of the Air Sinuses. The parts beneath the turbinate processes are indicated by stippled lines.

Latterly the sinus grows into and expands the presphenoid and part of the basi-sphenoid, the sphenoidal turbinate remaining as its anterior wall. The sphenoidal turbinate is a detached part of the ethmoidal cartilage.

It will thus be seen that all the nasal air sinuses are produced primarily by a budding outwards of the nasal mucous membrane into the cartilaginous basis of the lateral nasal processes. Disease may readily spread to these sinuses from the nasal cavities. By means of the sinuses the area of the face is increased to support the adult palate bearing the permanent teeth. Most of them open on the respiratory tract of the nasal cavity. They are ventilated with every breath. They act also as resonance chambers.

Vestigial Turbinates.—There is frequently to be seen in the adult one, or even two, secondary meatuses above the superior; these are constantly present in the chimpanzee and in mammals with a keen sense of smell. In the human foetus of four months six turbinates are usually present, besides secondary processes in the meatuses beneath them. The upper-

most of these, the sixth, becomes the sphenoidal turbinate; the fifth disappears; the third and fourth may remain separate or become united; the first and second form the inferior or maxillo-turbinal and middle turbinate processes. The agger nasi (naso-turbinal, Fig. 198), in front of the attachment of the middle turbinate process, is a vestige of the naso-turbinal, a process well developed in most carnivora and animals with a strong scent. The uncinate process, which forms the lower border of the hiatus semilunaris, is continuous at its base with the naso-turbinal. Through the hiatus semilunaris acting as a gutter, the antrum may become a cesspool for a suppurating frontal sinus.

Organ of Jacobson.¹—Mention has already been made of the organ of Jacobson—situated on the nasal septum above the naso-palatine canals. During development (Fig. 193) a part of the olfactory plate becomes detached, and is afterwards invaginated in a pocket in the septum and

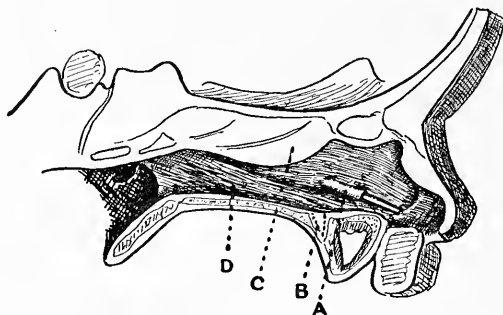


FIG. 200.—Nasal Septum of a Child at Birth, showing a rod inserted in the pocket of Jacobson's organ (A). B, closed naso-palatine canal; C, presphenoid; D, vomer.

guarded by a scroll of cartilage. It reaches its maximum development in the human foetus at the 5th month, and afterwards becomes a mere vestige—often unrecognizable. It sometimes persists and forms a very evident structure on the septum. A pocket can usually be seen on the septum at birth (Fig. 200). This special development of the olfactory organ is highly developed in all herbivorous vertebrates in whom the naso-palatine canals are widely open, and thus the juices and odours of the mouth have free access to the organ. Professor Broman² has suggested that it is for sampling substances dissolved in fluid, as is the case with the olfactory organ of fishes.

Nervus Terminalis.³—Amongst the fibres of the olfactory nerve, particularly in the branch to Jacobson's organ, there occur nerve cells, apparently of the same nature as those belonging to the sympathetic system. From these cells issue fibres which connect the olfactory areas of sense

¹ E. Zuckerkandl, *Ergebnisse der Anat.* 1908, vol. 18, p. 801.

² Ivar Broman, *Jubilee Festschrift of the University of Lund*, 1918.

³ For references to Literature see Olof Carsall, *Journ. Comp. Neur.* 1918, vol. 30, p. 1; R. McCotter, *ibid.* 1913, vol. 23, p. 145; H. Ayrers, *ibid.* 1919, vol. 30, p. 323.

epithelium with grey matter near the lamina terminalis of the fore-brain. The fibres constitute the nervus terminalis which is well developed in low vertebrates and of which there remains a vestige in man.

Nasal Duct.¹—Although in no way connected with the sense of smell, the nasal duct is closely related to the nasal cavities. It is formed between the lateral nasal and maxillary processes (Figs. 155, 193). It is laid down as a solid epithelial cord along the naso-maxillary groove at the end of the second month. It becomes canaliculized during the 3rd month.² Three bones bound it: the superior maxilla on the outer side, formed in the maxillary process; the inferior turbinate, formed in the cartilage of the lateral nasal process, and the lachrymal, formed over the lateral nasal cartilage, bound it on the inner side. The formation of the palate cuts the duct off from the mouth. The hamulus of the lachrymal varies much in size, and is the vestige of a large process, which in lower primates enters

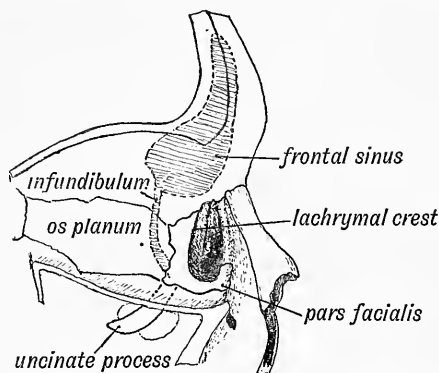


FIG. 201.—Showing on the Inner Wall of the Orbit (1) the Position of the Infundibulum, (2) the Pars Facialis Lachrymalis.

into the formation of the inferior margin of the orbit. This **pars facialis** sometimes occurs in man (Fig. 201). Occasionally the frontal and superior maxillary bones may push towards each other between the lachrymal in front and lateral mass of the ethmoid behind, and thus form a fronto-maxillary articulation on the inner wall of the orbit.

Malformations of the Nose.—In Figs. 156 and 166 two malformations of the nose are represented. In Fig. 156 the rare condition is shown in which one olfactory pit and its corresponding processes form a polypoid body; in Fig. 202 the condition of **cyclops**, where both nasal cavities are enclosed in a proboscis is represented. The eyes are also fused. The condition of the facial skeleton in such a case is represented in Fig. 166. In such cases there has been an arrest of growth of the cephalic end of the embryonic plate, with a fusion of the olfactory bulbs and also of the optic vesicles. The two olfactory plates and pits are united in a single median structure. In this condition we seem to have represented a pure develop-

¹ See references, p. 174.

² See Schaeffer, *Amer. Journ. Anat.* 1912, vol. 13, p. 1.

mental abnormality—not a reversion to some past stage in evolution (see p. 161).

Two other malformations require mention. During the 3rd, 4th and 5th months of foetal life an epithelial plug is formed within the anterior nares—where the cutaneous and nasal epithelial coverings meet. In

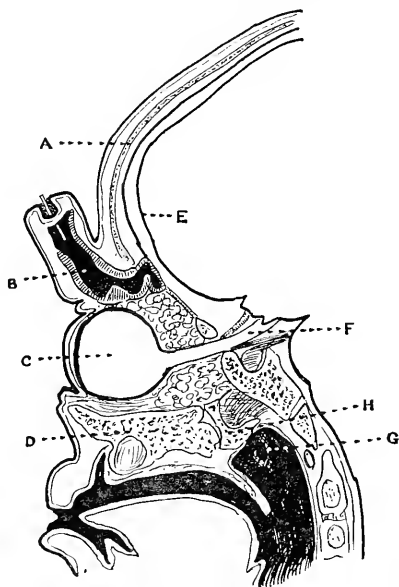


FIG. 202.—Median Sagittal Section of the Head and Face in a Case of Cyclops. *A*, frontal bone; *B*, single median nasal cavity contained in a proboscis formed by the nasal processes; *C*, median or fused eye; *D*, palate formed by the maxillary processes only; *E*, median cerebral vesicle; *F*, single optic nerve; *G*, Eustachian tube; *H*, palate bone.

rare cases the plug becomes organized, and forms a dense septum within the nares. A similar obstruction, often containing bone, may be formed near the posterior nares. The posterior narial occlusion represents an organization and persistence of the epithelial membrane which at first closes the primitive choanae (see p. 170).

CHAPTER XV.

DEVELOPMENT OF THE STRUCTURES CONCERNED IN THE SENSE OF SIGHT.

The Nature of the Eye.—It is in vain that we appeal to comparative anatomy for light on the various stages in the evolution of the eye; the eye of vertebrates is already fully formed in the earliest form known. Our knowledge of its origin and nature rests on an embryological foundation; during the 4th and 5th weeks of human development we see the eye compounded from three sources: (1) the retina and optic nerve arise as an outgrowth of the neural tube; (2) the lens arises from the ectoderm or body covering; (3) the tunics and mechanism of accommodation from the mesoderm. The union of these three tissues to form the most marvellous contrivance of the human body is a product of countless ages of evolution. A comparison with the olfactory organ, already mentioned in the last chapter, assists us in understanding the peculiar nature of the eye. The olfactory plates are neural in nature; their sensory cells give rise to the fibres of the olfactory nerves. The plaques of olfactory epithelium are situated near the open anterior end (neuropore) of the neural tube; one can easily understand how they might shift towards the neural tube, merge with it, and become enfolded with the part which forms the olfactory bulb. Were we to implant the olfactory epithelium in the olfactory bulb we should produce a structure comparable to the retina. During an early part of the 4th week the two retinal plates are represented by depressions on the sides of that part of the medullary folds which are enclosed to form the fore-brain (Fig. 203). The epithelium which lines the optic evaginations, clearly parts of the original surface covering of the embryo, does not become endodermal cells but, like the olfactory plates, gives rise to those highly modified sensory cells—rods and cones. Besides the rods and cones the optic evagination gives rise to nerve and other cells, in this respect resembling a typical part of the neural tube. It is thus clear that the olfactory and optic nerves are of a totally different nature to the other cranial nerves. We must seek the origin of the retina as a superficial sense organ, which has become so modified in the course of evolution that its primitive simple nature is hard to detect.

The **structures concerned in the sense of sight** are:

- (1) The Eyeball and the Optic Nerve;
- (2) The Eyelids and Lachrymal Apparatus;
- (3) The Orbit, and the Muscles, Nerves and Vessels contained in it;
- (4) The Nerve Centres and Tracts.

The Eyeball.—The condition of the eye in the 4th week of foetal life is shown diagrammatically in Figs. 203, 204. The three elements which unite to form the eyeball are as yet separate. They are :

(1) **Ectoderm**, which forms (a) the epithelium of the cornea, (b) the lens, and probably (c) the capsule of the lens.

(2) **Neuroderm**, which forms (a) the optic nerves, (b) sensitive retina, (c) pars ciliaris retinae, (d) uvea, (e) pigmentary layer of retina, (f) the hyaloid membrane.

(3) **Mesoderm**, which forms (a) outer tunic (sclerotic and fibrous cornea) ; (b) middle tunic (choroid, ciliary-choroid and iris) ; (c) the vitreous humour

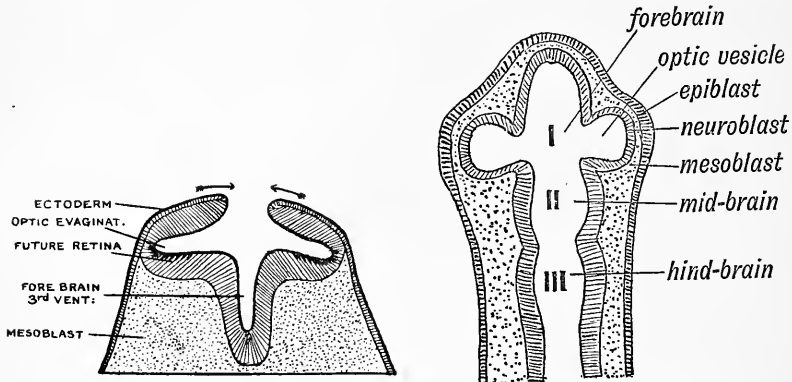


FIG. 203.—Diagrammatic Section across Fore-brain of a Human Embryo in early part of 4th week to show the Optic Evaginations. (After Professor Bryce.)

FIG. 204.—Diagram of the Elements which form the Eyeball.

1. **Structures derived from the Ectoderm.**¹ (a) **The lens.**—The lens is developed by a saccular invagination of the ectoderm situated over the optic vesicle at the beginning of the 5th week (Fig. 205). About a week later it becomes a closed sac by the severance of its connection with the ectoderm, its wall being formed by a single layer of epithelial cells. The cavity of the lenticular vesicle is gradually obliterated by the cells of the posterior wall becoming elongated (Fig. 206) until they reach the anterior wall (7th and 8th weeks). Each elongated cell is transformed into a lens fibre.

The cells of the anterior wall retain their primitive form (Fig. 206). New lens fibres are added by the cells at the margin (equator) becoming multiplied and elongated. The central fibres, which are formed first, are the shortest, the fibres of every additional layer produced become longer than those of the previous layer, hence the concentric arrangement of fibres. Further, the fibres of each layer are so graduated in length that, when produced, they meet along certain lines which radiate from the anterior and posterior poles of the lens. The lens is relatively large at birth, being two-thirds of its final size ; growth continues until puberty,

¹ E. Kallius, *Ergebnisse der Anat.* 1904, vol. 14, p. 234 ; 1906, vol. 16, p. 746 ; 1907 vol. 17, p. 463 (Development of Eye) ; F. Keibel, *Keibel and Mall's Manual of Human Embryology*, 1912, vol. 2.

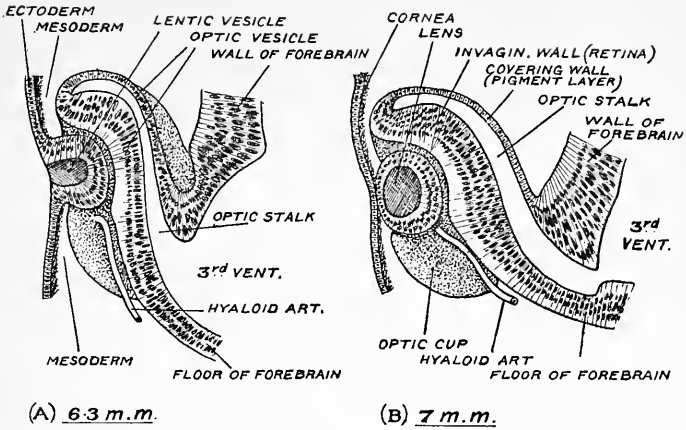


FIG. 205, A.—Depression of the Ectoderm to form the Lenticular Vesicle, early in the 6th week. (Hochstetter.)
 B.—Separation of the Vesicle later in the 6th week. Both figures represent Coronal Sections of the Fore-Brain and Optic Vesicle in Human Embryo. (After Hochstetter.)

and even then has not ceased, for Priestley Smith found that there is an appreciable addition to its weight with each decade of life. It will thus

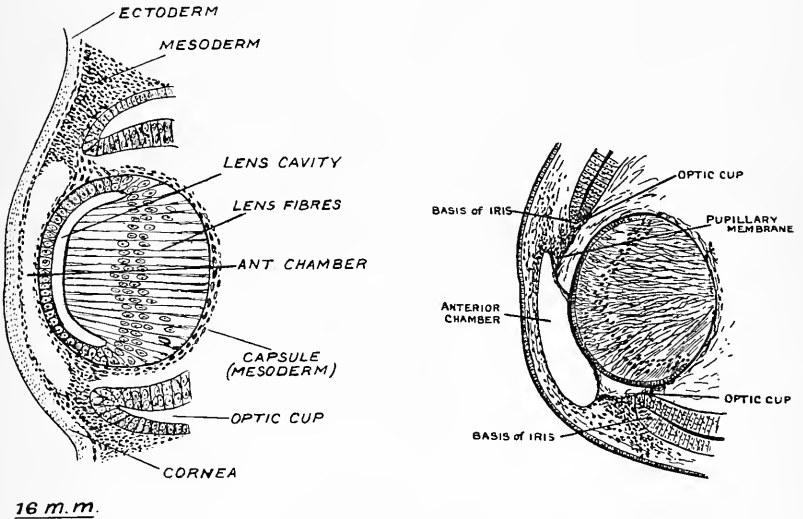


FIG. 206.—The Formation of the Lens Fibres from the Epithelium on the Posterior Wall of the Lenticular Vesicle and the ingrowth of mesoderm to form the substance of the Cornea and Vascular Capsule of Lens, 7th week. (After Lindahl.)
 FIG. 207.—Diagrammatic Section of the Anterior Part of the Eyeball to show the state of the Anterior Chamber and Iris in the 5th month. (After Broman.)

be seen that the lens is an area of modified epidermis, and in manner of development closely resembles the sense organs in the skin of fishes and amphibians. Like the epidermis, it shows a tendency in the aged to be

transformed into keratin. The oldest cells (the central or nuclear fibres) alter first; hence the central position of the cataract which occurs so frequently in old people.

(b) **The cornea.**—The epithelial covering of the cornea is continuous with the surrounding ectoderm. It becomes transparent. The mesoderm which grows in between the lens vesicle and ectoderm forms the connective-tissue basis of the cornea and, by a later invasion, the vascular capsule of the lens (Fig. 206).

(c) The capsule of the lens is a cuticular membrane formed by the lenticular cells. Outside the proper capsule a vascular tunic is formed from the mesoderm (Fig. 207).

2. **Structures formed from the Optic Vesicles (neurodermal element).**—Each vesicle is well developed soon after the commencement of the 4th

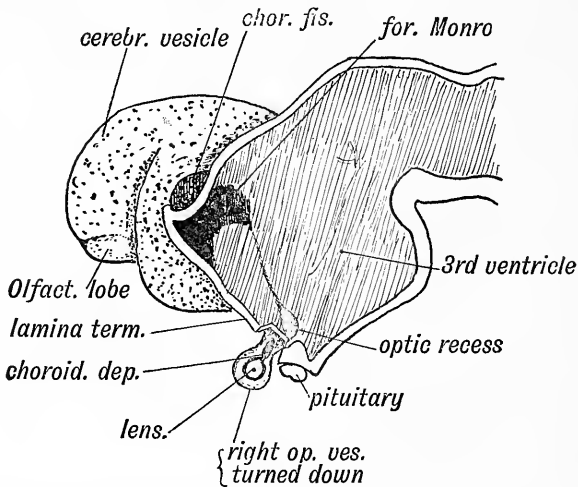


FIG. 208.—Diagram showing the connection with the Fore-Brain and condition of the Optic Stalk and Vesicle at the end of the 6th week of development. (After His.)

week (see Figs. 203, 204); even before the medullary plates have quite met to enclose the cavity of the fore-brain the optic vesicles have commenced as evaginations of those plates. They form a great lateral diverticulum on each side of the fore-brain—a cavity which becomes the third ventricle in the adult. The condition of the right optic vesicle at the end of the 6th week is shown diagrammatically in Fig. 208. The stalk or neck remains constricted to become the optic nerve while the vesicle enlarges and becomes invaginated to form the optic cup.

Invagination of the optic vesicle.—Almost as soon as it begins to grow out the optic vesicle becomes invaginated, one half being pushed within the other (Figs. 205, *A*, *B*). The lenticular bud lies within the indentation. The remarkable fact was discovered by Dr. Warren Lewis that the optic vesicle, if transplanted, can cause overlying ectoderm to produce a new lenticular bud. The invaginated vesicle is known as the **optic cup**. Fine

fibres unite the neuroblastic cells which line the optic cup with the deep aspect of the lenticular vesicle (Cirincione). The invagination of the vesicle, which takes place in an oblique manner—as if pressure had been applied from below and behind—leads to the closure not only of the cavity of the vesicle, but also to that of the distal half of the stalk (optic nerve). The point at which the central artery enters the optic nerve marks the upper limit of the invagination of the optic stalk (Fig. 209). By the 5th week the optic vesicle no longer communicates with the cavity of the fore-brain, but the recessus opticus in the floor of the third ventricle, above the chiasma, remains to mark the point at which the original evagination took place (Fig. 208). The parts formed from the optic vesicles are :

(a) **The optic nerve** is formed from the stalk of the optic vesicle. The wall of the stalk is at first composed of a single layer of columnar epithelium ; in the second month these cells produce a sponge-work of fibres on the surface of the stalk.¹ During the 8th week, the optic fibres, developed as

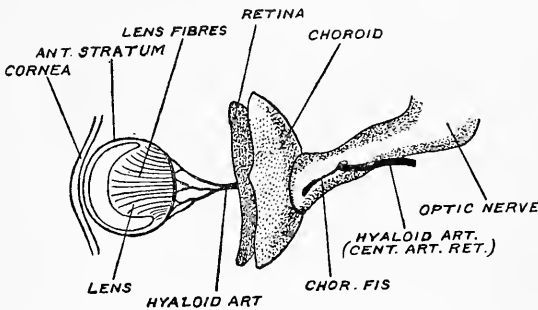


FIG. 209.—Certain parts of the Eye during the 7th week of development. (After His.)

processes of the neuroblasts of the invaginated layer, begin to grow into the brain from the retina along the sponge-work of the optic stalk.² Thus are formed the greater number of the fibres in the optic nerve. The optic fibres also form the chiasma in the floor of the third ventricle and the optic tracts on the wall of the fore-brain (Fig. 224). It will thus be seen that the optic nerves and vesicles are of the same origin as the cerebral vesicle—both representing modified parts of the wall of the fore-brain.

(b) **The pigmentary layer of the retina** is formed from the ensheathing or outer layer of the optic cup (Fig. 210). At first the wall of the optic vesicle is composed of a single layer of epithelium ; the outer or pigmentary layer of the retina retains this embryonic form. Pigment appears as early as the 6th week, commencing at the marginal border.

(c) **The uvea** is the layer of pigmented epithelium which covers the posterior surface of the iris. It is formed out of both outer and inner layers of the optic cup, and represents the rim of the cup (Fig. 211).

(d) **The pars ciliaris retinae** is formed out of that part of the inner or invaginated layer of the optic cup which lies in the shadow of the iris, and

¹ Prof. Robinson, *Journ. Anat. and Physiol.* 1896, vol. 30, p. 319.

² Prof. Cameron, *Journ. Anat. and Physiol.* 1905, vol. 39, p. 135.

is therefore inaccessible to light rays. It also retains the primitive columnar or partly transitional form of the epithelium (Fig. 211). The ora serrata marks the junction of the pars ciliaris retinae and sensitive retina.

Ciliary Processes.¹—At the commencement of the 4th month, the pars ciliaris retinae becomes plicated or puckered into 60 or 70 small folds

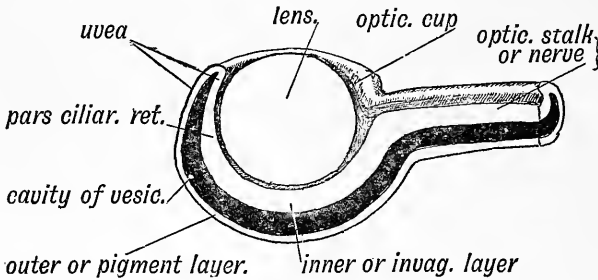


FIG. 210.—Diagrammatic Section of the Optic Cup and Lens. The cavity is represented as gaping, whereas from the 5th week onwards the outer and inner walls are in contact.

(Fig. 211); mesoderm of the middle tunic (choroid) grows into the puckers and forms the ciliary processes. It should be observed that the lens lies within the optic cup and the ciliary processes are formed round the equator or circumference of the lens. The retinal epithelium which covers the ciliary processes is secretory in nature. It forms the aqueous humour, thus

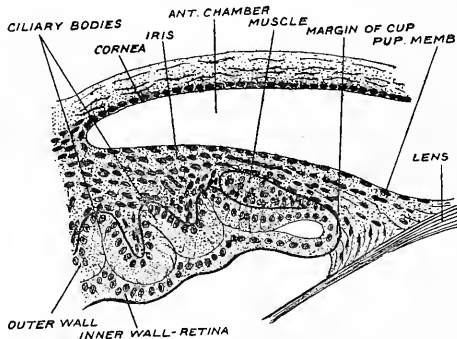


FIG. 211.—Section of the Iris, showing the folding of the marginal part of the Optic Cup to form the ciliary processes and the origin of the Sphincter Muscle of Iris from the anterior or outer layer of cup, in Human Foetus in 6th month. (Szily).

recalling the ependyma, which covers the choroid plexuses of the ventricles of the brain. It is strange that from the same layer as gives origin to nerve cells there should also arise supporting (neuroglial) and secretory cells, and as we shall see anon, the unstriped muscle of the iris (Fig. 211).

(e) **The sensitive retina** is formed out of the inner or invaginated layer of the optic cup (Fig. 212). At first the inner wall is composed of a single layer of epithelium. The ciliary part of the retina retains this form. What

¹ M. von Lenhossék, *Verhand. Anat. Gesellsch.* 1911, p. 81 (Dev. of Ciliary Body).

is called the **outer** aspect of the primitive retina is directed towards the pigmented layer, but is separated from that layer by what remains of the cavity of the optic vesicle (Fig. 210). That cavity, it will be remembered, is a prolongation of the neural canal or ventricular cavity of the brain. The **inner** or vitreous aspect of the retina, corresponding to the outer

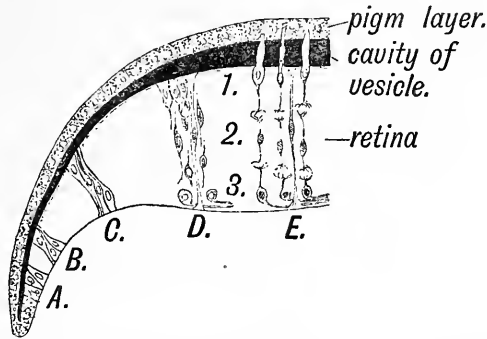


FIG. 212.—Diagrammatic Section across Optic Cup to show the manner in which the Cells of the Inner Layer of the Optic Cup are differentiated to form the Retina. (After Fürst.)

A, B, C, D, E, show stages in the development of the Retina from the simple layer of Cells.

1. The outer stratum of Sense Cells (rods and cones).
2. The middle stratum connecting (bipolar) Nerve Cells.
3. The inner stratum of Ganglionic Cells and Fibres.

The cavity of the Optic Vesicle, which is closed by the invagination of the retinal layer within the cup and obliterated by the outgrowth of the rods and cones, is represented by a wide black zone in the diagram.

aspect of the neural tube, is directed towards the lens. The manner in which the complicated strata of the retina arise from the single layer has been investigated by Professor Fürst, and is represented diagrammatically in Fig. 212. Differentiation starts at the centre of the optic cup and spreads towards the periphery. The original layer, while dividing and producing

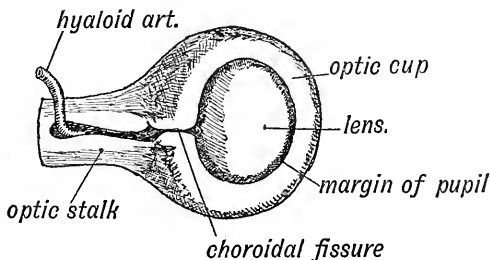


FIG. 213.—The Optic Stalk and Cup, viewed on the lower and lateral aspect, showing the Closure of the Choroidal Fissure.

broods of cells, still retains its position, the daughter cells being pushed towards the vitreous aspect of the retina, and by the middle of the 7th month of foetal life all the retinal elements are present, the fovea centralis being the last feature to appear. As far as mammals are concerned the fovea centralis is a characteristic of the higher primates.

On each surface of the retina is developed a cuticular or **limiting membrane**. Some of the original epithelial cells are elongated between the limiting membranes and form the fibres of Müller. On passing from the margin of the cup to its centre all stages will be seen between the single layer and the multi-stratified condition. Ultimately three strata can be recognized in the retina. Beneath the outer limiting membrane the original cells remain as the retinal sense epithelium; processes from these cells break through the outer limiting membrane to form the rods and cones; the middle stratum forms bipolar cells; beneath the inner limiting membrane ganglionic cells are formed. The middle stratum by its processes links together the sense epithelium and the ganglionic cells, and thus stands in the same relationship to the sense epithelium and ganglionic cells as a posterior root ganglion does to the touch corpuscles of the skin and the cuneate and gracile nuclei of the medulla. In many ways the development of the retina recalls the development of the spinal cord. Both form part of the neural tube.

The Choroidal Fissure.—Occasionally congenital fissures are seen in the lower segment of the iris (coloboma iridis) or choroid (coloboma choroidea) (Fig. 214). A white line, due to absence of pigment, may be seen in the corresponding segment of the retina when the interior of the eye is examined. These are due to imperfect closure of the choroidal fissure. The choroidal fissure is the result of the peculiar mode in which the optic vesicle is cupped or invaginated. The lens grows into it from the malar or lower lateral aspect and becomes lodged in the anterior part of the depression; the posterior part becomes the choroidal fissure (Fig. 209).

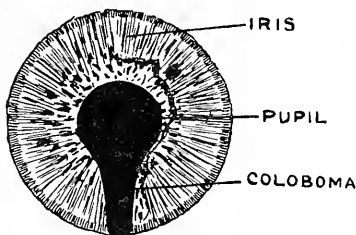


FIG. 214.—Coloboma or Cleft of Iris. (After Seggel.)

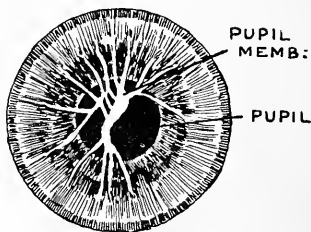


FIG. 215.—Remains of Pupillary Membrane. (After Prof. Hippel.)

The margins of the fissure unite, fusion commencing near its middle and spreading distally to the margin of the cup and proximally until it reaches the point of entrance of the hyaloid artery (Fig. 209). By the 8th week all traces of the fissure should have disappeared. Its union recalls the closure of the fissures in the upper lip. Coloboma and harelip are lesions of a similar nature. With the closure of the choroidal fissure the optic cup is completed. Its brim or margin becomes the site of the pupil.

Binocular Vision.—At first the optic vesicles are directed laterally in the human embryo, and in mammals generally the eyes are so directed, each eye having its own field of vision. In the Primates the eyes swing forwards during the second month; binocular vision is thus made possible. With

binocular vision and the combination of images appear in the highest primates :

- (1) A fovea centralis and macula lutea (L. Johnston) ;
- (2) A partial crossing of the optic fibres at the chiasma ;
- (3) Certain alterations in the attachments of the oblique muscles of the eyeball.

The primitive cavity of the Optic Vesicle (Fig. 210) is of some clinical importance. It is obliterated by the invagination of the vesicle ; the rods and cones formed in the inner or invaginated layer grow out across the cavity into the outer or ensheathing pigmented layer of the retina (Fig. 212). From accident or disease the retina may be detached, thus causing blindness ; the separation takes place between the pigmented epithelium, which remains *in situ*, and the rods and cones, which fall inwards with the nerve layer. Fluid then collects in the site of the primitive cavity of the optic vesicle. The optic part of the medullary plate in amphibian embryos has been transplanted and produced a retina in its new site. Some experimenters found that the ectoderm over the optic graft gave rise to a lens.¹

3. Parts of the Eyeball formed from the Mesoderm.—After the optic vesicle has been invaginated against the lens, a continuation of the same layer of mesoderm, which surrounds and forms the coverings of the brain, envelops the optic cup and spreads inwards between the ectoderm and the lens. As may be seen from Figs. 205, *A*, *B*, the lens at first lies in contact with the inner or retinal wall of the optic cup, no mesoderm intervening. When they move apart in the 3rd month a connecting network of fibres appears between them.

The structures formed from the mesoderm are :

(1) **The vascular tunic of the lens.**—While the choroid fissure is still open, mesodermal tissue passes into the cup and in it is formed the hyaloid artery, which is enclosed, when the lips of the fissure fuse. Mesodermal cells also enter by the pupillary margin (Fig. 206), and in this way the actively growing lens becomes surrounded by a *vascular tunic*, in which the hyaloid artery terminates. Beneath this tunic lies the proper capsule of the lens, which is formed from the epithelium of that body.

(2) **The vitreous humour** is formed out of the mesoderm which passes into the optic cup behind the lens. Kölliker was of opinion that the mesodermal cells were absorbed and that the vitreous was wholly produced from the lenticulo-retinal fibrillar network mentioned in a previous paragraph. The closure of the choroidal fissure cuts the vitreous humour off from the mesoderm which covers the outer layer of the optic cup and becomes transformed into the tunics of the eyeball. The vitreous humour—like Wharton's jelly of the umbilical cord—represents an early form of embryonic tissue. It consists of cells embedded in a jelly-like matrix.

(3) **The hyaloid artery** is the vessel which supplies the mesodermal tissues within the optic cup ; it terminates in the vascular capsule of the lens

¹ Most of these instructive experiments have been carried out by American investigators. For a recent list of researches see Spemann, *Zool. Jahrbuch*, 1912, vol. 32, Heft 1. W. H. Lewis, *Amer. Journ. Anat.* 1907, vol. 7, p. 259.

(Figs. 209, 216). In the 7th month foetus a trace of the artery can still be seen passing through the vitreous humour from the optic disc to the lens. With the gradual obliteration of the artery, the mesodermal capsule of the lens becomes thin and clears up. A foetus born in the seventh month is blind, because the vascular capsule of the lens has not quite disappeared. The anterior part of the capsule—filling the pupil—is the **membrana pupillaris**. A trace of the membrane may occasionally be seen crossing the pupil (Fig. 215). The part of the hyaloid artery within the optic nerve persists as the central artery of the retina. The canal of the artery

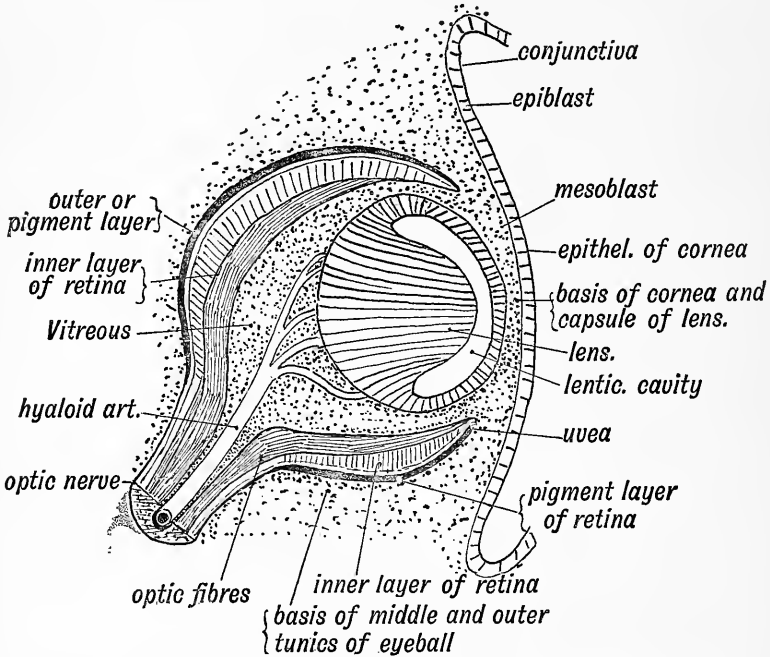


FIG. 216.—Diagrammatic Section of the Eye showing the parts formed from the Mesoblast or Mesoderm. (After His' Model of the Eye of a 3rd month human foetus.)

within the vitreous humour, from the optic disc to the lens, remains as the **hyaloid canal**—a lymph path. The hyaloid artery may persist and cause partial or complete blindness. It disappears some days after birth in cats and rabbits.

(4) **The aqueous chamber** is formed between the cornea and lens, its walls being entirely of mesodermal origin. In Fig. 216 the mesoderm which invades the space between the ectoderm and lenticular vesicle is represented as forming not only the basis of the cornea but also the anterior wall of the vascular tunic of the lens, these two parts being supposed to become separated by the formation of the aqueous chamber. Dr. Lindahl¹ finds, however, that these two parts are formed separately, the mesodermal basis

¹ *Anat. Hefte*, 1915, vol. 52, p. 195.

of the cornea in the 6th week and the lenticular capsule later—at the 9th week, the aqueous chamber being the potential chamber between these two formations (Fig. 206). Fluid begins to collect in the pupillary area of this space in the 6th month and spreads, so that in the 7th month the chamber has extended to the corneo-scleral junction. Almost to the time of birth, the anterior chamber of the aqueous is very shallow (Fig. 217), the lens lying near the cornea. Even so late as the 6th month (see Fig. 207) the posterior part of the aqueous chamber—the part which lies between the iris in front and the lens behind—is not opened up. We must regard the aqueous system as strictly comparable to the cerebro-spinal and not as part of the lymph system.

(5) **The choroid, ciliary processes and iris** form the middle or vascular tunic of the eye, and are developed out of the mesoderm which covers

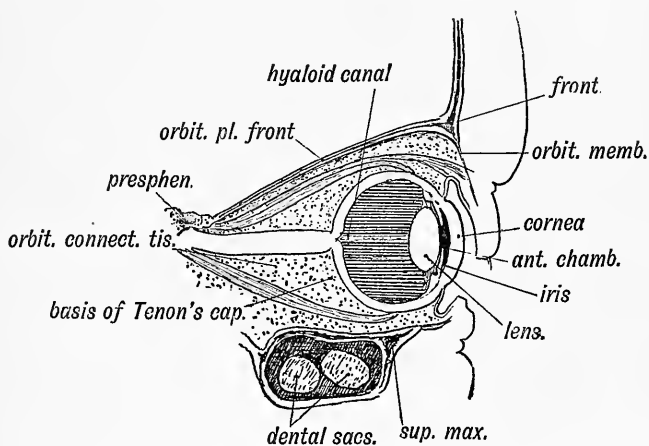


FIG. 217.—Section of the Eye and Orbit at birth.

the optic cup. They form a vascular and pigmented covering through which the optic cup is nourished, and correspond to the combined pia mater and arachnoid membranes of the brain. The ciliary muscle is formed in this tunic in the 4th month. The iris is late in its development. The uvea on its deep surface is formed from the brim of the posterior surface (Fig. 211). In the 6th month the sphincter, and then the dilator muscles, are produced—their origin being peculiar. The muscle fibres arise from the epithelial cells of the uveal part of the optic cup (Fig. 211). The iris is fully formed in the 7th month and can then react to light.

(6) **The sclerotic** is derived from the outer mesodermal envelope of the optic cup and is strictly comparable to the primitive cranial capsule. It is continuous in front with the cornea; behind, with the sheath of the optic nerve and dura mater. In some vertebrates, but not in mammals, plates of bone are developed in the anterior half of the sclerotic, recalling the deposition of dermal bones in the primitive capsule of the brain.

The tapetum lucidum is absent in the human and primate eye. It gives the metallic lustre seen on the retinal surface of the eye of the ox, and is

formed by a layer of fine fibres which are developed on the retinal surface of the choroid.

(7) **The capsule of Tenon**, the bursa or connective-tissue socket of the eyeball, is developed in the mesoderm surrounding the eyeball. A lymph space separates it from the sclerotic, which is but slightly marked until after birth. The **choanoid muscle** (retractor bulbi or orbital muscle) which surrounds the sclerotic part of the eyeball as a muscular hood in mammals and vertebrates generally and arises in common with the external rectus, has become greatly reduced in man and the higher primates. Remains of the retractor bulbi—a striated muscle—have been described by Prof. Whitnall in the human orbit.¹ The *unstriated muscle of the orbit* occurs in two places; the **orbital part** (Müller's muscle) bridges the sphenomaxillary fissure; the palpebral part forms the non-striated musculature found in the insertions of the levator palpebrae (Groyer). The non-striated muscle is supplied by sympathetic nerves. Its function is obscure, but is probably designed to regulate the pressure and circulation of the venous blood of the orbit.

Growth of the Eyeball.—The eyeball is relatively large at birth, its diameter (17-18 mm.) being three-fourths of the adult diameter (24 mm.). In rate and precocity of growth it is comparable to the brain. The macula-lutea and fovea centralis are said to have reached their full size at birth. A child born at the end of the 7th month is sensitive to light and darkness; appreciation of form comes towards the end of the 1st year, while colours are not recognized until the 2nd or 3rd years—or in some cases the colour sense is not developed. The colours at the opposite ends of the spectrum (red-violet) are the first to be recognized (Edridge Green).

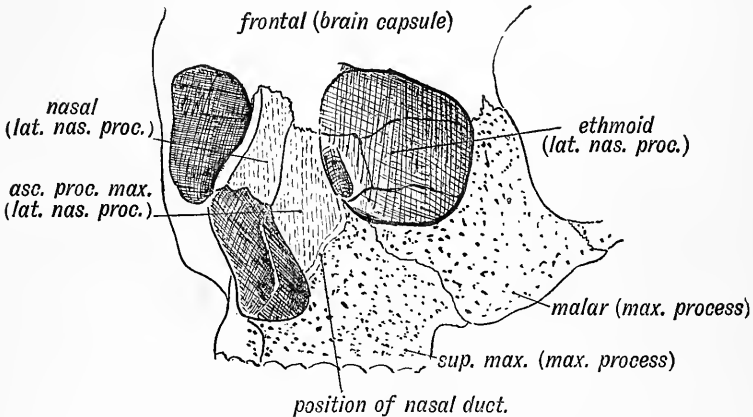


FIG. 218.—The Origin of the Bones entering into Formation of the Orbit.

Formation of the Orbit (Fig. 218).—The orbit is formed (1) above by the capsule of the fore-brain in which the frontal bone is developed; (2) externally and below by the maxillary process. In the maxillary process the malar bone and superior maxilla (except the ascending nasal process)

¹ *Journ. Anat. and Physiol.* 1912, vol. 46, p. 36.

are developed. (3) The inner wall is formed by the lateral nasal process, in which the nasals, lachrymals and lateral mass of the ethmoid, are formed. The optic nerve enters the orbit between the orbito- and pre-sphenoids, both of which help to form the orbit. The orbital surface of the great wing is formed at a later period in a membranous basis (see Fawcett, p. 135). The **orbital plate** of the malar cuts the orbit off from the temporal fossa ; it is developed in higher primates only. The nasal duct is formed between the maxillary and nasal processes (Figs. 154 and 219). In lower primates and mammals generally the hamular process of the lachrymal appears on the margin of the orbit ; the **pars facialis lachrymalis** is sometimes seen in the human skull (Fig. 154, p. 160). Mention has been made of the division of the orbital region of the primitive skull (Fig. 133)

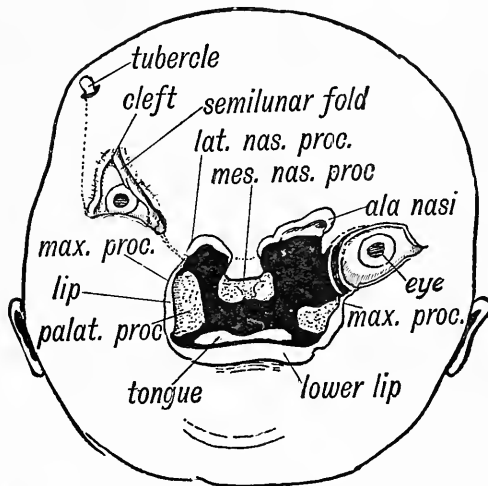


FIG. 219.—Malformed Face of a newly born Child in which the Double Formation of the Eyelid is seen. The Lateral Nasal and Maxillary processes have not fused. Two folds separate the Eye from the Nasal Cavity. The inner fold represents the Caruncula Lachrymalis and the outer the Plica Semilunaris.

into orbital and temporal parts during the evolution of the temporo-mandibular joint (see page 139). The division is effected by the upbuilding of a lateral wall to the mammalian orbit ; the lateral orbital wall must be regarded as part of the bony scaffolding for giving attachment to the muscles of mastication.

The eyelids are formed in the earlier weeks of the 3rd month by folds of ectoderm which commence above and below the superficial part of the eyeball. Mesoderm grows into the folds and forms the tarsal plates. The upper eyelid is formed from the capsule of the fore-brain, the lower from the maxillary process. About the middle of the 3rd month the edges of the lids meet, adhere, and remain adherent until the end of the sixth month. In rabbits, mice, kittens and puppies the lids are still closed at birth. The upper eyelid is developed in two parts—outer and inner ; occasionally a notch remains on the margin, and marks the point at which the two parts unite (Fig. 219). The upper end of the plica semilunaris

is attached in the embryo at the position of the notch. The ectoderm on the deep surface of the lids retains a columnar shape, and forms the palpebral conjunctiva. It is continuous with the ectodermal stratum of the cornea. From the ectoderm between the adherent edges of the lids, buds grow during the 4th and 5th months, and form the eyelashes, Meibomian and other glands, in the same manner as hairs and sweat glands are developed. The Meibomian glands represent modified sebaceous glands, but the hair or cilia from which they primarily arose have vanished. The curious epicanthic fold is shown in Fig. 220. It is represented in all races during foetal life.

The *plica semilunaris* (Fig. 221), a fold of conjunctiva in the inner canthus of the eye, is a vestige of the third eyelid (*membrana nictitans*) which is fully developed in birds and reptiles. In the snake's eye Mayou found that this membrane formed what is commonly called the anterior

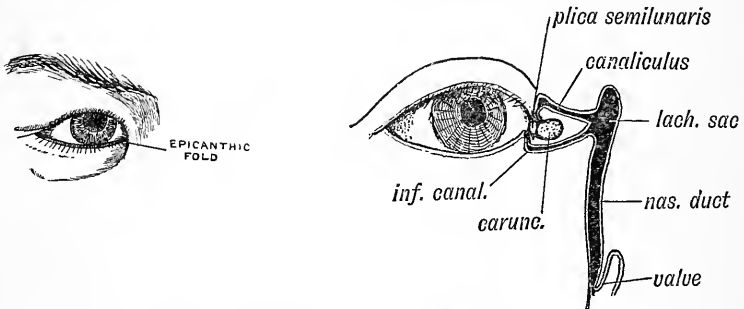


FIG. 220.—Epicanthic or Mongolian fold. (After Meckel.)

FIG. 221.—Diagram of the Plica Semilunaris and Lachrymal Canaliculi.

lamina of the cornea; it is the epithelium of this membrane which desquamates and renders the animal temporarily blind. The *plica semilunaris* is relatively large in the human foetus, reaching its maximum development in the 5th month. It is well seen in the cat, partially crossing the cornea as the lids are shut. The lachrymal papillae in man rub in the grooves at the outer and inner margins of the fold.

The **Lachrymal Gland**¹ arises at the beginning of the 3rd month as a number of ectodermal buds which spring from the fornix of the conjunctiva beneath the upper lid, and grow into the tissue of the outer and upper segment of the orbit (Fig. 222). The outer buds form the orbital part of the gland; the more internal buds form the palpebral part. Smaller lachrymal glands may occasionally be found at the outer angle of the eye, which is the position occupied by the lachrymal glands of birds and reptiles (Wiedersheim). The lachrymal canaliculi and sac and nasal duct are formed out of solid epithelial cords enclosed between the maxillary and lateral nasal processes (see p. 201). The canaliculi are formed during the 3rd month as sprouts from the upper end of the solid rod of epithelium repre-

¹ Development of lachrymal gland, F. Ask, *Anat. Hefte*, 1910, vol. 40, p. 489, 1908, vol. 36, p. 189.

senting the nasal duct. While the bud of the upper canaliculus opens at the inner end of the upper lid (Fig. 222, *A*), the inferior canaliculus extends some way along the lower lid before it comes to the surface (Ask). It may form a secondary communication nearer the inner angle of the eye, thus giving rise to a congenital lachrymal fistula. With the formation of the

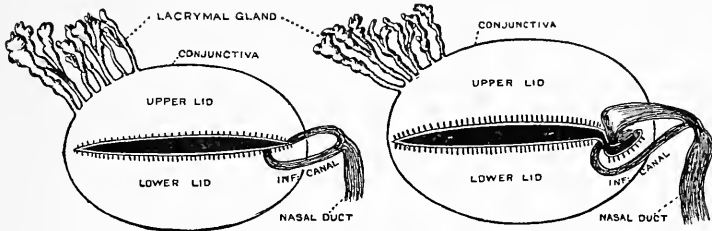


FIG. 222, *A*.—Showing the Termination of the Lower Lachrymal Canaliculus some distance from the Mesial End of the Lower Eyelid, in a foetus 2 months old. The tubular outgrowths of the lacrimal gland are also shown.

B.—The Mesial Extremity of the Lower Eyelid cut off to form the Caruncula. The lachrymal outgrowths are more complex in structure. From a foetus in 4th month of development. (After Ask.)

lachrymal canaliculus, part of the lower eyelid is cut off and forms the caruncula (Fig. 222, *A* and *B*).

The Orbital Muscles.¹—We have already seen that the head is composed of nine segments, at least four of these being occipital; also, that each segment gives rise to a muscle plate (Fig. 149). The muscle plate

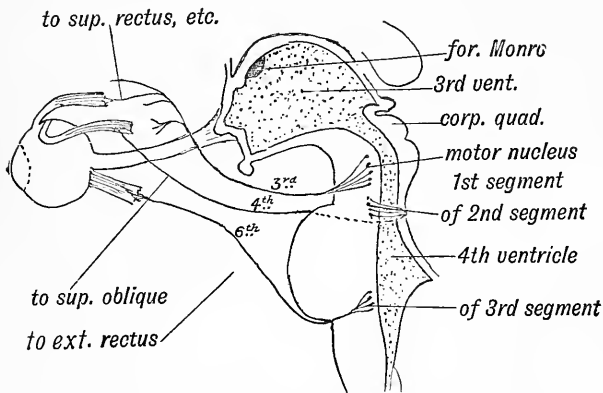


FIG. 223.—Diagram of the Motor Nerves of the Muscles of the Eye derived from the 1st, 2nd, and 3rd Cephalic Segments.

of the maxillary or premandibular—usually called the first—segment forms the muscles supplied by the third cranial nerve—which is the motor nerve of that segment. The mesencephalon (crura cerebri) contains the corresponding segment of the neural tube. The ciliary muscle and sphincter

¹ For an account of the development of orbital vessels see F. Dedekind, *Anat. Hefte*, 1909, vol. 38, p. 1. See also Dr. Eliz. A. Fraser, *Proc. Zool. Soc.* 1915, p. 299.

of the iris also belong to this segment, and are supplied by the IIIrd nerve (Fig. 223). The muscle plate of the mandibular, usually named the second head segment, produces the superior oblique. The dorsal decussation of the IVth nerves is evidently the result of a mutual migration of their nuclei—following Kapper's neuro-biotactic law. The muscle plate of the hyoid or third cephalic segment gives rise to the external rectus; the Vth nerve is the nerve for the somatic musculature of the segment, the VIth supplying the splanchnic muscles.

The sensory nerves of these three segments are fused together in the three divisions of the Vth nerve. The ciliary ganglion is the splanchnic (sympathetic) ganglion of the premandibular segment. The nerves for the retractor muscle, the non-striated muscle of the upper eyelid, and the dilator fibres of the iris, issue from the upper three dorsal segments of the spinal cord, and reach the eye by the cervical sympathetic chain and cavernous plexus. The nerve fibres for the orbicularis palpebrarum pass out with the facial, but they are said to arise from, or have connection with, cells in the first segment of the neural canal (oculomotor nucleus). The ophthalmic division of the fifth represents the sensory somatic nerve of the same segment to which the third nerve belongs; hence the reflection of pain along this nerve (frontal headache) in disorders of accommodation, the muscle of accommodation being the ciliary, and its nerve, the oculomotor, both also derivatives of the first segment. Mention has been made of the origin of the retractor muscle with the external rectus from the 3rd segment. The levator palpebrae superioris is a late delamination from the superior rectus.

Development of the Nerve Centres concerned with Sight.—Five parts of the brain are concerned with vision. They are:

- (1) The optic tracts.
- (2) The basal centres surrounding the termination of the aqueduct of Sylvius in the 3rd ventricle.
- (3) The optic radiations.
- (4) The occipital lobes—in part at least.
- (5) The angular gyri.

(1) **The optic tracts** are made up of fibres developed from the ganglionic cells of the retina and also in part of efferent fibres developed from cells of the basal ganglia in which the optic tracts are seen to terminate. The fibres grow in by the optic stalk, those from the nasal fields of the retina decussating in the floor of the third ventricle between the origins of the optic vesicles, and thus form the chiasma. The optic fibres grow backwards on the surface of thalamencephalon (see Fig. 224) and on the optic thalamus to reach the nerve centres which afterwards form the pulvinar, lateral geniculate bodies and the superior corpora quadrigemina. In these centres the optic fibres end. It is said that 80 per cent. of the fibres from the central area of the retina terminate in the lateral geniculate bodies.

(2) **The basal ganglia.**—**The corpora quadrigemina.**—Almost in every structure the human embryonic condition resembles the adult condition of lower vertebrates. A good example is seen in the corpora quadrigemina

The human foetus at the end of the 2nd month (Fig. 224) shows the corpora quadrigemina represented by a prominent thickening in the roof of the cavity of the mid-brain, which forms subsequently the aqueduct of Sylvius. The thickening is divided into lateral halves by a median sulcus, each half being nearly as large as the cerebral vesicle of that period. In Fig. 225 is shown the condition in an adult lizard; there is one body on each side—the **optic lobes** or corpora bigemina. As the human foetus grows older, each lateral lobe becomes divided into an upper and lower part by the formation of a transverse groove, the upper and lower pairs of the corpora quadrigemina being thus formed. The upper pair are connected with sight. In the mole they are vestigial, but in compensation the inferior

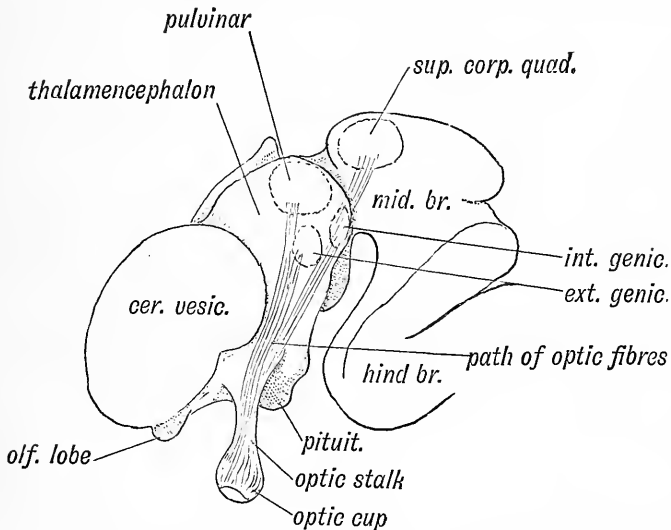


FIG. 224.—Diagram of the Foetal Brain at the end of the 2nd month, showing the position in which the Optic Tracts are developed.

corpora are well developed as they are connected with the sense of hearing, which is very acute in that animal.

The pulvinar and lateral geniculate body, in which the upper division of the optic tract ends, are developed in the wall of the 3rd ventricle (thalamencephalon). The mid-brain is the part primarily connected with sight; in the floor of its cavity—the aqueduct of Sylvius—are situated the motor nuclei for the muscles of the eye; on its roof—the terminal centres for the optic tract (see p. 95). As the vertebrate scale of animals is ascended, the termination of the optic tracts is found to be transferred more and more to the centres on the thalamencephalon. The projection of retinal stimuli to the occipital cortex from the nucleus of the pulvinar is shown in Fig. 113.

(3) **The optic radiations**¹ connect the basal optic centres just named with the mesial surface of the occipital lobes, and *vice versa*. The fibres

¹ For fuller details of optic tracts see Prof. Elliot Smith, *Cunningham's Text-Book of Anatomy*.

join the posterior part of the internal capsule, and pass under and round the posterior horn of the lateral ventricle to end in the cortex of the calcarine fissure and neighbourhood. The cortex in which the optic radiations terminate is divided by a narrow white stratum—the **line of Gennari**—into a superficial and deep layer.

(4) **The occipital lobe and calcarine fissure.**—A mesial view of the 5th month foetal brain is shown in Fig. 226. The occipital lobe is already well

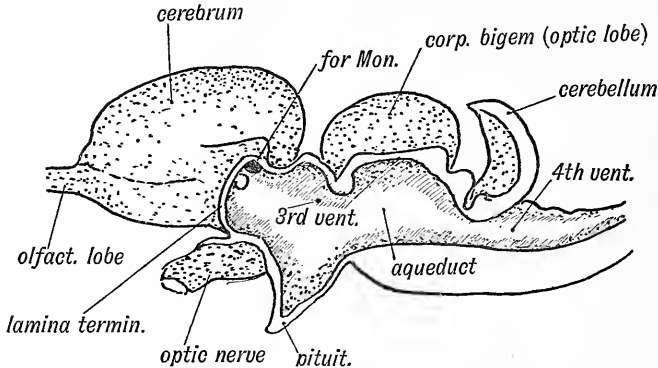


FIG. 225.—Mesial Section of the Brain of a Lizard, showing the resemblance to the Human Foetal Brain (Fig. 224), especially in the development of the Corpora Bigemina.

formed ; its inner aspect shows the calcarine and parieto-occipital fissures. A section across the occipital lobe is shown in Fig. 226 ; the posterior horn is large ; the calcarine fissure indents its inner wall, giving rise to the

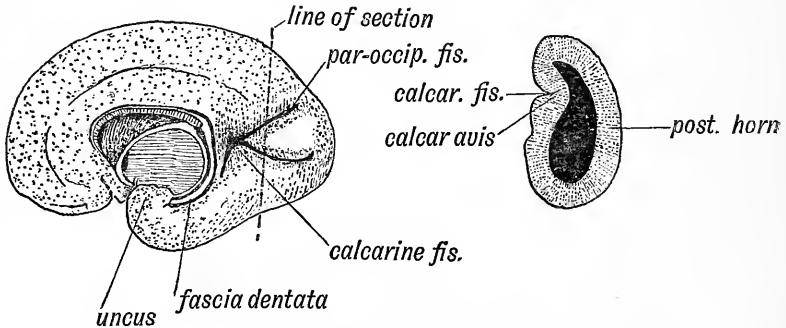


FIG. 226, A.—View of the Mesial Surface of the Brain in the 5th month.
B.—Section of the Occipital Lobe at the position marked in A.

calcar avis or hippocampus minor, a feature which is seen in the brains of nearly all mammals (Elliot Smith).

The **calcarine** is one of the first fissures to be formed on the brain ; it appears early in the fifth month. This and the hippocampal depression, which is connected with the sense of smell, are the two fissures most commonly present in the mammalian brain. The posterior part of the calcarine fissure is a later formation, and is distinguished as the retro-

calcarine (see Fig. 127, p. 131). The optic radiations end in the cortex of the retro-calcarine fissure.¹ In Fig. 227 the condition of the occipital lobe in the 5th week is shown. The lateral ventricle is as yet undifferentiated into horns, and only the rudiment of the occipital lobe is present. The occipital lobe is produced by a backward growth of the cerebral vesicle, the posterior horn being produced as a diverticulum of the cavity of the vesicle. By the 5th month the occipital lobe has reached far enough back to overlap the cerebellum. The striate or visuo-sensory area of the human brain is not larger than that of the anthropoid ape, but the association or visuo-psychic area is infinitely more extensive. "Thus, we can take it that the superiority of the human over the ape's brain as a psychical organ must be the result mainly of the higher development of the association or peri-striate areas" (Elliot Smith).

(5) **The angular gyrus** is connected with the calcarine region by association fibres. In it are seated the word-seeing and word-understanding

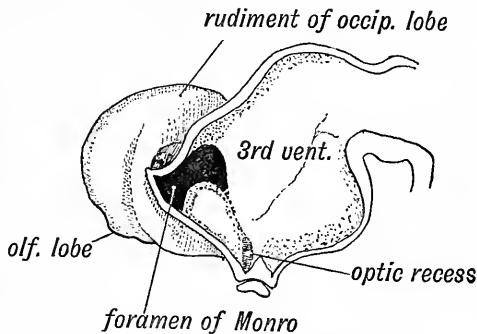


FIG. 227.—Mesial Section of the Brain at the 4th week, showing the rudiment of the Occipital Lobe. (After His.)

centres. It is developed round the posterior end of the 1st temporal or parallel fissure (Fig. 123). It is part of the wall of the cerebral vesicle. The first temporal or parallel fissure appears during the sixth month and is one of the primary fissures. It is found in the brains of all primates except the lowest.

Summary.—It will thus be seen that three parts of the neural tube are specialized in connection with sight.

(1) The optic vesicle, an outgrowth from the fore-brain (thalamencephalon).

(2) The occipital region of the cerebral vesicle, which receives fibres projected from the basal nuclei connected with the eyes.

(3) The walls of the 3rd ventricle (thalamencephalon) and mid-brain (mesencephalon), in which the terminal nuclei of the optic fibres are developed.

The tunics of the eye are extensions of the embryological coverings of the brain. The choroid coat and the vitreous humour spring from the

¹ For a description of the cortex of the visual areas see Elliot Smith, *Journ. Anat. and Physiol.* 1907, vol. 41, p. 237. See also references on p. 116.

same layer as forms the pia mater and arachnoid. The sclerotic is a prolongation of the primitive cerebral capsule, in which the skull bones are formed. The optic vesicle carries with it a prolongation of the arteries and veins of the fore-brain. Part of the optic vesicle is transformed into a secretory epithelium over the ciliary processes in the same way as the wall of the neural tube becomes a covering for the choroidal villi of the brain.

CHAPTER XVI.

THE ORGAN OF HEARING.

The Nature of the Labyrinth.—It often happens, when we seek to interpret the developmental changes which give rise to an organ or system of the human body, that a reference to the condition seen in certain groups of fishes—especially those belonging to the shark kind, selachians—gives us great assistance. This is true as regards the organ of hearing. In a shark or ray every part of the internal ear—the labyrinth with its semi-circular canals—is already evolved with the exception of one part—the canal of the cochlea ; it is represented by a mere rudiment. The labyrinth of the shark is not an organ of hearing, for it is generally admitted that fishes are insensitive to sound-waves, but for the balancing or orientation of the body. Most men who have investigated the nature of the labyrinth of fishes agree that it represents a specialization of one of a series of superficial sense organs set on the sides of fishes—the organs of the lateral line—these also being connected with the functions of balancing and movement. Hence we find that the labyrinth begins as a pocket-like invagination of the ectodermal covering in the head region. The essential element of the labyrinth is its ciliated epithelium ; movements of the cilia, produced in various ways, give rise to stimuli which pass by the VIIIth nerve to the hind-brain. The auditory or cochlear part of the labyrinth appeared when the land-forms of vertebrates were evolved. In vertebrates above fishes the rudiment of the cochlea begins to be differentiated and an apparatus for converting sound waves into mechanical waves in the labyrinth is evolved.¹ A vibrating drum was established in the site of the first of the pharyngeal or visceral clefts. We must also suppose that in the piscine type, which gave origin to the ancestry of the mammals, the mammalian form of mandible was already evolved, for it is from remains of the primitive cartilaginous skeleton of the lower jaw that the malleus and incus are differentiated in the human and mammalian embryo.

The Structures which form the Organ of Hearing.—In Fig. 228 is shown diagrammatically the derivation of the five elements which unite together to make up the organ of hearing. The five elements are :

(1) The **otocyst**—an area or plaque of ectoderm covering the head of the embryo above the first visceral cleft which becomes invaginated in a saccular

¹ G. L. Streeter, *Journ. Experiment. Zoology*, 1906, vol. 3, p. 543 ; 1907, vol. 4, p. 431 ; 1914, vol. 16, p. 149 (Results of Experiment on Developing Internal Ear) ; A. Keith *Proc. Roy. Soc. Med.* 1919, vol. xiii. p. 1 (Otological Section).

form, to become the epithelial lining of the membranous labyrinth. Some of its lining cells become differentiated into ciliated sensory epithelium.

(2) A **ganglion** of somewhat uncertain origin, one view being that it arises from the neural crest as is represented in Fig. 228, but there is a growing conviction that some at least of the ganglionic cells arise from the ectoderm of the otocyst. The nerve cells form the cochlear and vestibular ganglia. Each cell sends out two processes, one to become connected with the epithelium of the otocyst, the other to end in groups of nerve cells in the floor of the hind-brain, their collective fibres forming the VIIIth nerve. The development of the auditory nerve thus resembles that of the posterior or sensory root of a spinal nerve.

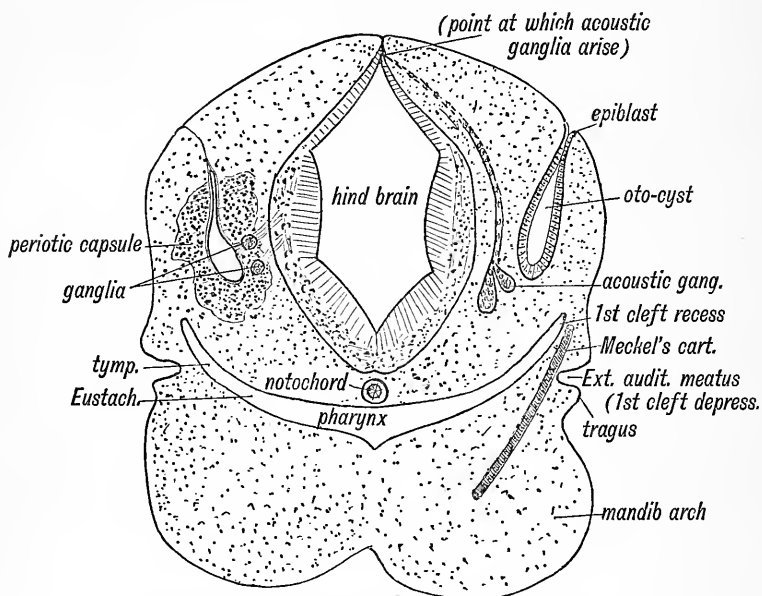


FIG. 228.—Diagrammatic Section through the Cephalic Region of an Embryo, showing the origin of the Auditory System.

(3) The otocyst (membranous labyrinth) becomes surrounded by a capsule of cartilage—the **periotic capsule**. This ossifies from several centres, and forms the bony labyrinth and petro-mastoid.

(4) The Eustachian tube, the tympanum and antrum of the mastoid arise in connection with the pharyngeal pocket between the mandibular and hyoid arches; the corresponding external cleft depression forms the point of origin for the external auditory meatus; while out of the tissue between the internal pocket and external cleft, representing in position a "cleft-membrane," is formed the membrana tympani.

(5) The **hyomandibular cartilage** (Fig. 173), which served primarily to bind the cartilages of the maxillary process, mandibular and hyoid arches to the base of the skull, becomes the stapes. The incus and malleus arise from the upper end of the mandibular bar of cartilage (Fig. 132).

In fishes the auditory apparatus is composed of the three elements named first. In amphibians, reptiles and birds a membrana tympani is developed, which is connected with the inner ear by an unjointed derivative of the hyomandibular cartilage, *the columella*. In mammals a tympanic cavity, external auditory meatus, and auditory ossicles appear.

External Auditory Meatus.—A section along the external meatus of a newly born child shows that it is divided by a constriction into outer and

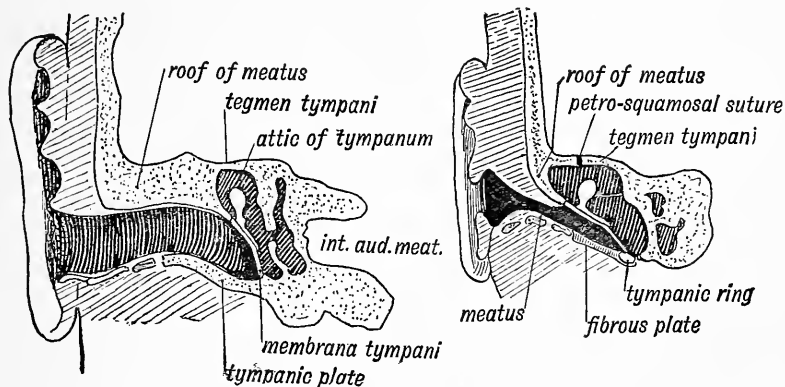


FIG. 229, A.—A Section of the External Auditory Meatus of the Adult.
 B.—A Section of the External Auditory Meatus at Birth. (After Symington.)

inner parts (Fig. 229, B). The outer part is derived directly from the first cleft depression ; the inner part arises during the 2nd and 3rd months by a solid ingrowth of epithelium which, commencing from the cleft depression or pit, grows inwards until it comes in contact with the handle of the malleus, when it expands to form the fundus of the meatus (Figs. 230, 236).

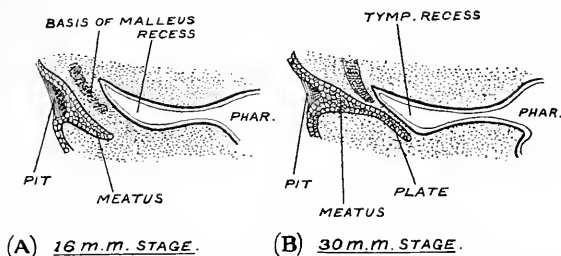


FIG. 230.—Showing the growth of the external meatal plug and its relationship to the tympanic recess of the pharynx. (Prof. Frazer.)

During the 7th month the deeper part of the meatus and outer aspect of the drum are formed by a breaking down of the central, and therefore older, cells of this ingrowth. Cartilage surrounds the part of the meatus derived from the cleft ; the floor of the deeper part is formed at birth by a fibrous plate continuous with the tympanic ring. In the adult the tympanic ring has grown outwards in the fibrous tissue, as we have already seen (p. 178), to form the tympanic plate and the inner two-thirds of the

meatal floor. The squamous part of the temporal, which is developed in its roof, also grows outwards, and forms a thick, horizontal plate in the inner two-thirds of the meatal roof (Fig. 229, *A* and *B*). Over the roof lies the third temporal convolution.

The meatus is supplied in front by the nerve of the mandibular arch (auriculo-temporal branch) and also by a branch from the nerve of the hyoid arch—the facial. Why the vagus should supply it with a branch (Arnold's nerve) is obscure. In fishes a branch of the vagus passes backwards beneath the skin on each side and supplies the sense organs of the lateral line. Many regard the auricular branch of the vagus as a vestige of such a branch.

In the newly born child the membrana tympani is so obliquely set that its outer surface is almost in contact with the meatal floor (Figs. 229, *B*, 236). With the development in length of the meatus, it becomes more

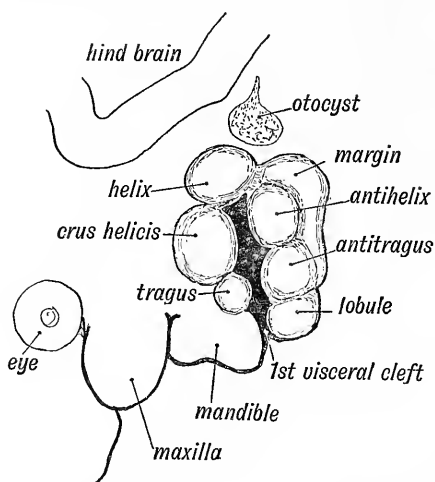


FIG. 231.—Showing the Tubercles which arise round the First Visceral Cleft to form the External Ear.

vertical in position. The deeper part of the meatus may fail to form, or the whole cleft may become closed. In such a case there is commonly a corresponding absence of development of the middle and internal ear.

The External Ear.—Six tubercles appear on the mandibular and hyoid arches round the 1st cleft depression during the 6th week and form the basis of the external ear (Figs. 231 and 232). Three of these tubercles grow from the mandibular arch and form the tragus, crus of the helix, and helix; three from the hyoid to form the lobule, antitragus and antihelix. The posterior margin of the ear, or descending helix, with the lobule, arise as a mere thickening or elevation of the skin behind the tubercles on the hyoid arch. During the latter part of the 2nd month and first part of the 3rd, the pinna begins to assume its definite form. The tubercles of the helix and antihelix send out processes which cross the upper part of the cleft and obliterate it, while the neighbouring tubercles fuse to form

the definite parts of the ear. The posterior margin and lobule rise up at the same time as a free fold. The auricular tubercles may not fuse completely and thus leave fistulae between them. Such fistulae are commonly seen between the tragus and root of the helix, or between the antihelix and the helix. The mandibular part of the auricle is supplied, as one would expect from its origin, by the third division of the 5th, while the sensory fibres for the hyoid part come from the 2nd cervical by the great auricular and small occipital nerves.

Darwin's Tubercle.—The human ear appears to be derived from a form in which the margin was pointed at the posterior superior angle, such as is seen in many of the lower forms of apes and mammals generally. With the retrogression of the posterior border or descending helix and increased development of the antihelix in the human ear, the posterior margin became infolded; hence the tip appears as a tubercle on the inturned

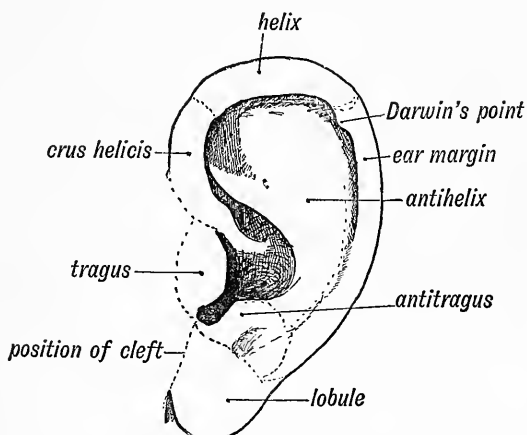


FIG. 232.—Showing the part of the Adult Ear formed by each Tubercle.

posterior margin or welt of the human ear (Fig. 232). The small size and restricted mobility of the external ears of higher primates result from the free manner in which these animals can turn their heads in the direction of sounds.

Muscles of the External Ear are derived from the platysma sheet and are supplied by the nerve of that sheet—the 7th or facial. The part of the platysma sheet which surrounds the external meatus and acts on the ear appears to have been the first of the facial muscles to be evolved. The ear muscles are not so reduced in man as in some other primates, such as the orang.

The Eustachian Tube.—The Eustachian tube has usually been regarded as a derivative of the first of the inner cleft recess—a diverticulum of the lining membrane of the primitive pharynx between the mandibular and hyoid arches (Fig. 198, *A*). Recently Professor Frazer¹ has made a

¹ *Journ. Anat.* 1914, vol. 48, p. 391.

thorough enquiry into its development, and has found that its origin is more complicated than was supposed. In Fig. 233, *A*, the left half of the floor of the pharynx of a human embryo, five weeks old, is represented. Between the 1st and 2nd and between the 2nd and 3rd arches the lining mucous membrane of the pharynx is seen to dip outwards and at first is actually in contact; as yet there is no sign of Eustachian tube or of tympanum. In Fig. 233, *B*, the opposite half of the floor of the pharynx of a human embryo towards the end of the 2nd month of development is shown; the basis of the Eustachian tube and tympanum is now apparent as a wide recess between the first and third arches, the hyoid arch being squeezed outwards on the outer wall of the recess. The oblique fold forming the roof and posterior wall of the Eustachian tube is formed by the forward

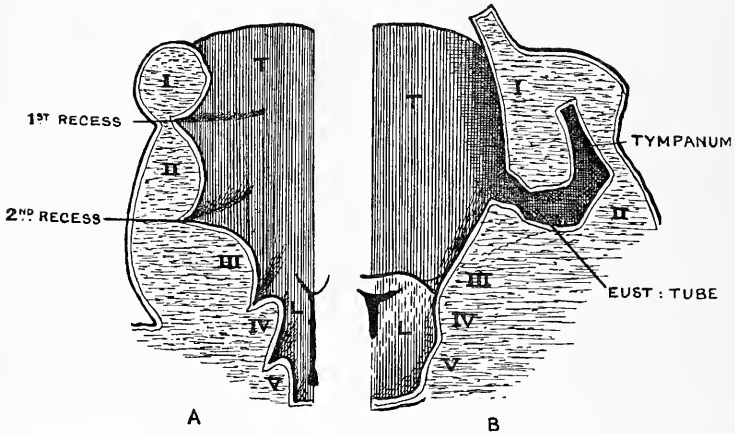


FIG. 233.—Figures illustrating the Development of the Eustachian Tube and Tympanum. (After Prof. Frazer.)

- A*.—The Floor of the Pharynx of a Human Embryo five weeks old. The visceral arches are cut across and the inner cleft recesses indicated.
B.—The Floor of the Pharynx of a Human Foetus seven weeks old, showing the origin of the Eustachian Tube by an Evagination of the Pharynx opposite the 2nd or Hyoid Visceral Arch. *T*, rudiments of tongue on floor of pharynx; *L*, larynx.

growth of the substance of the 3rd arch, which, it will be remembered, also contributes to the formation of the soft palate. The Eustachian tube retains through life the ciliated epithelial lining of the primitive pharynx. Its inner two-thirds is bounded behind by a triangular plate of cartilage, which is attached at its inner or pharyngeal end to the internal pterygoid plate, by its outer to the tympanic ring, both of which are probably derived from the palato-quadrata bar (Fig. 173, p. 172). The cartilage is developed in the 4th month of foetal life. The tympanic plate grows inwards and forms the floor of the outer third of the tube (Fig. 235), while the petriotic capsule (petro-mastoid) which is developed above and behind the 1st cleft, grows forwards and forms the roof of its outer third. The part of the petro-mastoid which grows over it is the **tegmen tympani** (Fig. 229); it also forms the roof of the tympanum and of the antrum of the mastoid. The tensor tympani and tensor palati are developed on the mandibular side

of the first cleft and are supplied from the nerve of the mandibular process through the otic ganglion.

The Tympanum.—The tympanum can scarcely be said to exist until the 3rd month of foetal life. Until then, the Eustachian recess ends in jelly-like tissue containing the cartilaginous bases of the malleus and incus. It is directed outwards and backwards between the petiotic capsule to its posterior and inner side, and the external cleft depression (meatus) and developing squamosal to its outer (Fig. 234). As the tympanic recess, in which are represented both 1st and 2nd pharyngeal pockets, extends outwards and backwards, the gelatinous tissue is absorbed, so that, in the later months of development, the malleus and incus and developing stapes,

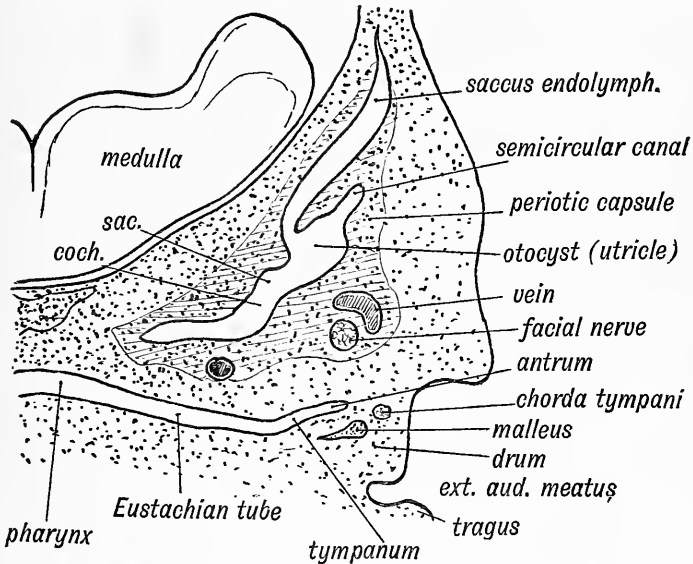


FIG. 234.—Showing the condition of the Auditory Organs in a 7th week Human Foetus. (After Siebenmann.)

with the chorda tympani, become surrounded by the entodermal lining of the recess and thus appear to lie within the cavity thus formed—the tympanum. The tympanic plate forms the floor of the tympanum, the membrana tympani and squamosal its outer wall, while the petro-mastoid forms its inner wall and roof (Fig. 235). The nerve of the 2nd arch—the facial—lies in its inner or mesial wall. That part of the tympanum which lies above the level of the membrana tympani is named the **attic**, and contains the head of the malleus and body of the incus (Fig. 229).

In carnivora and some other mammals the floor of the tympanum, formed by the tympanic plate, is inflated into a bulla, the tympanic bulla. Its meaning is unknown, but when a bulla is developed the antrum of the mastoid is small or absent.

Auditory Ossicles.—In the 3rd month the auditory ossicles become clearly differentiated in cartilage in the mesodermal tissue between the

meatal recess on their outer side and the Eustachian recess on their inner. Concerning their development, the exact researches of Broman,¹ of Hammar, and of Jenkinson² give us a very full account. The malleus represents the upper or articular end of Meckel's cartilage (Figs. 237, 132); the incus, developed beyond the articular end of Meckel's cartilage, represents the

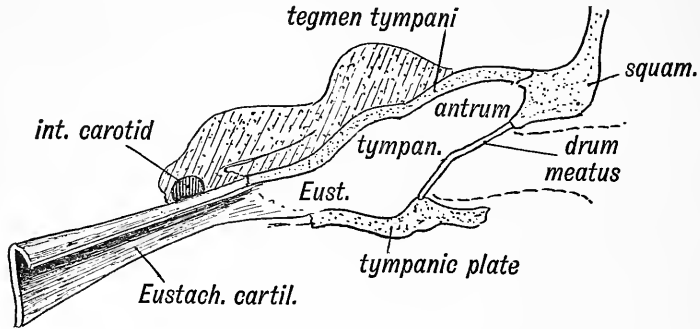


FIG. 235.—Showing the Cavities derived from the Eustachian Recess of the Primitive Pharynx.

cranial articular base—the quadrate of lower vertebrates. The stapes (Fig. 237) is developed at the upper end of the hyoid arch, the sides of the stirrup being formed round the dorsal end of the artery of the hyoid arch. Even in the 4th month of development the cavity of the tympanum has only reached the handle of the malleus (Fig. 236). The upper part of the drum

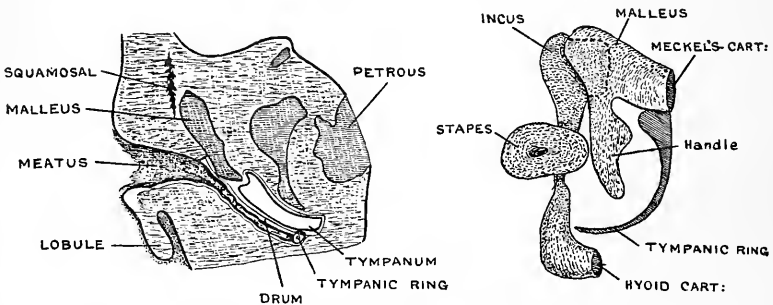


FIG. 236.—Section of the External Auditory Meatus, Drum and Tympanum of a Human Foetus in the 4th month of development. The meatal plug fills the deep part of the meatus and only the handle of the hammer is in the tympanic cavity. (After Broman.)

FIG. 237.—The Auditory Ossicles of the Left Side, seen on their Inner Aspect, during the 3rd month of development. (After Broman.)

(pars flaccida) is not yet differentiated. The attic, antrum, head of the hammer, and body of the incus are still outside the cavity of the tympanum.

The Antrum of the Mastoid represents the extreme outer or posterior end of the chamber derived from the extension of the Eustachian recess

¹ See Broman's excellent *Normale und abnormale Entwicklung des Menschen*, Wiesbaden, 1911.

² J. W. Jenkinson, *Journ. Anat. and Physiol.* 1911, vol. 45, p. 305; Hugo Frey, *Anat. Hefte*, 1911, vol. 44, p. 363.

(Figs. 234 and 235). It is formed during the 6th and 7th months by an expansion of the tympanic cavity upwards and backwards in the surrounding mucoid tissue. Its use is uncertain, but it has frequently to be exposed by the surgeon to remove the effects of chronic middle-ear disease. At birth its outer wall is formed by the thin post-auditory part of the squamosal (Figs. 238 and 239). The squamosal forming its outer wall is then only 2 mm. thick, but every year until the 20th, or later, this plate increases nearly 1 mm. in thickness, so that by the 20th year the antrum is buried by a plate of bone about 20 mm. thick. There is a great individual variation, however, in the thickness of its outer wall. The antrum lies above and behind the level of the external auditory meatus; the post-auditory spine and supra-meatal triangle formed by the post-auditory part of the squamosal lie over it and serve as surface guides to it. The antrum opens in front into the attic of the tympanum. The tegmen tympani (Fig. 239) forms its roof and the petro-mastoid its floor and inner wall. The canal for the VIIth nerve runs down the inner wall of its mouth

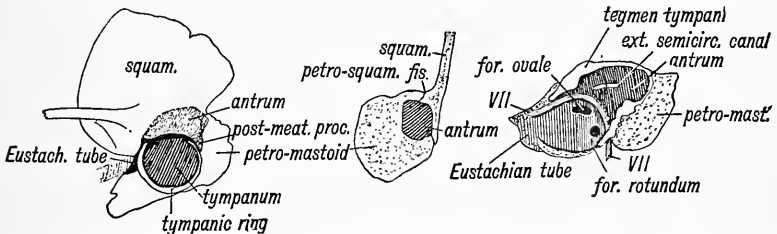


FIG. 238.—The Temporal Bone at birth, showing the formation of the Antrum between the Squamosal and Petro-mastoid.

FIG. 239.—A Transverse Section showing how the Walls of the Antrum are formed.

FIG. 240.—Showing the outer aspect of the Petro-mastoid at birth after the Squamosal is removed.

(Fig. 240), and in its inner wall is situated the external semicircular canal. The petro-squamosal suture in its roof (Fig. 239) and the masto-squamous suture on its outer wall (Fig. 181, p. 179) become closed the second year, and thus the escape of pus from it is rendered more difficult. The rudiments of the mastoid cells are already present as evaginations or pits of the antral lining at birth (Arthur Cheatele).

Petro-Squamous Sinus.—We have seen (page 133) that the primitive vein of the head, part of which persists as the cavernous sinus, escapes from the cranial cavity just in front of the auditory capsule. Before escaping from the skull it receives a tributary from the hind-brain—which afterwards occupies the petro-squamous suture. This vein, frequently of considerable size, runs forwards from the lateral sinus, and commonly ends in a tributary of the middle meningeal vein. It receives as it runs along, venules from the antrum and attic and may be the means of carrying infection from the middle ear to the lateral sinus or to the meningeal veins (Cheatele). The petro-squamous sinus may open in man, as it does in mammals generally, at the post-glenoid foramen, situated at the outer end of the Glaserian fissure, near the base of the zygoma. The vein thus emerging may represent the primitive vein of the head.

The Membrana Tympani.—As may be seen from Figs. 230, 234, the membrana tympani is of very considerable thickness until the gelatinous tissue in the tympanum is absorbed. It has an inner covering of entoderm and an outer of ectoderm. In the mesodermal tissue between the coverings lie parts of the malleus, incus and chorda tympani. As the gelatinous tissue round the fundus of the Eustachian recess is absorbed during the later months of foetal life, the tympanic lining membrane expands, and thus the handle of the malleus and chorda tympani come to appear as if they lie on the membrane, although really within it (Fig. 236). The mucous lining of the tympanum covers them. The membrane is supported by the tympanic ring, the age changes of which have already been dealt with (p. 178). The membrane contains tissue derived from both mandibular and hyoid arches, and hence receives nerves and vessels from both.

The Membranous Labyrinth.—The various parts of the membranous labyrinth of the internal ear are represented in Fig. 241. It consists of (1) the utricle; (2) three semicircular canals opening into the utricle; (3) the saccule; (4) a canal uniting the utricle and saccule—from, or near which, springs the ductus endolymphaticus. All of these parts constitute the vestibular or balancing part of the labyrinth. (5) The cochlear canal—the part connected with hearing. The labyrinth, although a complicated structure, has a very simple beginning. The cells of a certain area of ectoderm, situated above and behind the first cleft and lying against the

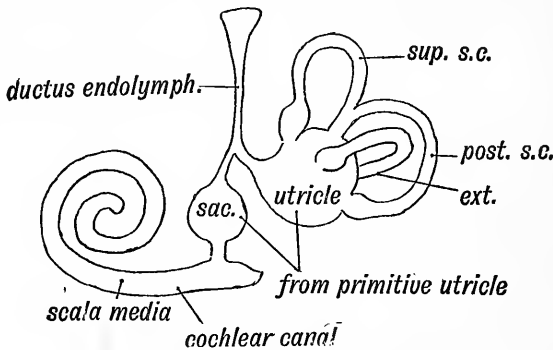


FIG. 241.—Diagram of the Membranous Labyrinth.

4th and 5th neuromeres of the hind-brain (Figs. 80, 93, 231) become invaginated during the 4th week. In this manner, and at this early date, there is formed a simple closed pyriform sac, the **otocyst**, which lies above the first visceral cleft and is soon surrounded by the mesodermal tissue which forms the primitive capsule of the cephalic part of the neural canal. The sac contains a fluid, the endolymph, and also otoliths are found in it later. The otocyst lies at first close to the side of the hind-brain with the ganglionic mass belonging to the 7th and 8th cranial nerves to its inner and anterior side (Fig. 93). The epithelial cells lining it, all of which are originally columnar, soon become flattened, except at the maculae acoustica,

where they retain the columnar form and develop hair-like processes. The hair-like processes are to serve as levers and become capable of being moved by various means to evoke nerve stimuli. Under the influence of gravity otoliths serve to move them; so do the currents in the semicircular canal as the head is moved and, so too, do the movements of the stapes. The hair cells become connected with the hind-brain by the auditory nerve fibres of the cochlear and vestibular ganglia. The otocyst clearly represents a sense organ which was primarily situated in the skin and through its hair-like processes was sensitive to the position and movements of the body. Its auditory function arose at a later stage.

In the lower vertebrates, as in the earlier embryonic stages of the higher mammals, the otocyst is of a saccular form with a stalk above—the **ductus endolymphaticus** (Fig. 242). The simplest form of vertebrate otocyst is seen in the lamprey; the superior and posterior semicircular canals are

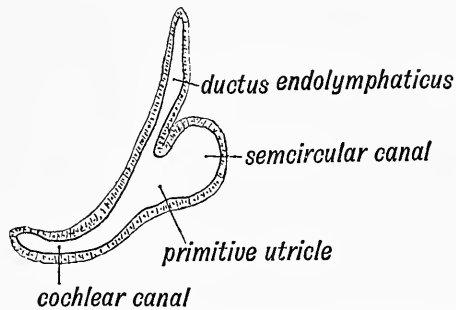


FIG. 242.—The Otocyst in an Embryo of five weeks; it shows a demarcation into the various parts of the Membranous Labyrinth.

present, but, as in the mammalian embryo, the primitive cyst is undivided into utricle, saccule and cochlear canal. The semicircular canals grow out from the vesicle as flat, hollow plates, but only the circumferences of the plates persist, the centres disappearing.

The development and differentiation of the human otocyst has been closely studied by Prof. Streeter.¹ In Fig. 243 three stages depicted by him are represented. At the 5th week there are three parts: (1) the ductus endolymphaticus, at one time regarded as the stalk which connected the cyst with the surface of the head, but now known to be an outgrowth formed after the stalk is obliterated; (2) the vestibular pouch or part; (3) the cochlear pouch or rudiment. At the 6th week a higher stage of differentiation is reached; all the parts of the adult labyrinth are indicated—the ductus and saccus endolymphaticus (both of uncertain import), the semicircular canals, with their ampullae; the utricle and saccule. All of these are derived from the vestibular part of the otocyst. The cochlear rudiment has extended into a bent canal, and its communication with the saccule is constricted to form the canalis reuniens. In the 10th week all the various parts are present, almost in their adult form.

¹ *American Journal of Anatomy*, 1907, vol. 6, p. 139; 1907, vol. 7, p. 337 (Development of Ganglia of vii, viii).

The utricle and saccule are now separated and only communicate by means of the ductus endolymphaticus. The cochlear canal has assumed its spiral form.

The **primitive utricle** or vestibular pouch, which represents the main part of the otocyst, subdivides into the saccule and utricle (Fig. 243, *C C'*, *C''*). The division occurs at the entrance of the endolymphatic canal, which thus comes to open into both saccule and utricle. The endolymphatic duct is enclosed in the petro-mastoid, its extremity appearing at the hiatus vestibuli, where it ends beneath the dura mater in a dilatation. The cochlear canal (scala media), the real auditory part of the labyrinth, although late in point of evolution, is not late in its developmental appearance. There is merely a rudiment of the cochlea in fishes and other amphibians. In reptiles, birds and monotremes it is a straight canal—

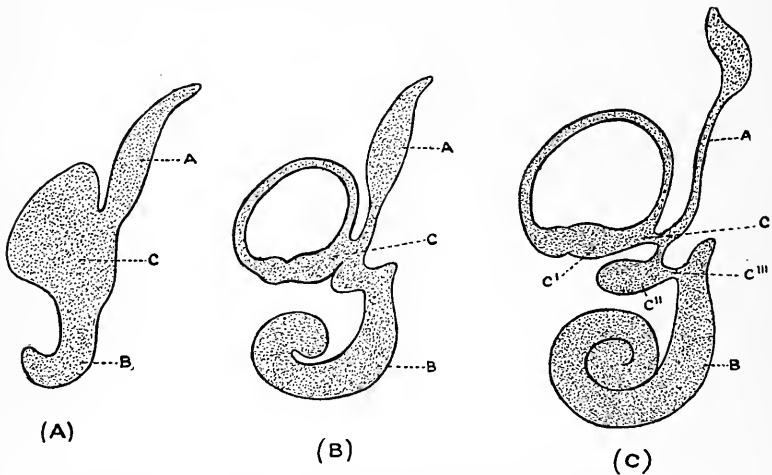


FIG. 243.—Three stages in the development of the Human Membranous Labyrinth. *A*, at the end of the 5th week; *B*, at the end of the 6th week; *C*, at the end of the 10th week. (Streeter.)

the **Lagena**. Only in mammals is it arranged spirally. In it the organ of Corti is developed.

Periotic Capsule.—The mesoderm surrounding the membranous labyrinth and dorsal aorta (internal carotid) above the first visceral cleft becomes cartilaginous at the end of the 2nd month of foetal life, forming the periotic capsule (Figs. 228, 234, 139). There are two centres of chondrification, one for the vestibular part—surrounding the vestibular division of the labyrinth, and one for the cochlear part—surrounding the cochlea. The course of the facial nerve indicates approximately their line of union. The cartilage of the cochlear part fuses with the parachordal or basilar cartilage; the vestibular part becomes continuous with the occipital plate (see p. 137).

Perilymph System.—The tissue which immediately surrounds the membranous labyrinth does not undergo chondrification, but becomes converted into an open meshwork of cells, the intercellular spaces

containing perilymph. The chief or *vestibular* cistern of the perilymphatic system is formed round the saccule and utricle. In its tympanic or outer wall (Fig. 240) there is an oval area in which the *fenestra ovalis* and foot plate of the stapes are formed. Streeter¹ found that the vestibular cistern is the first to form, commencing at the stapedial plate when the foetus is 50 mm. in length (11 weeks old); an extension grows out along one side of the cochlear canal to form the *scala vestibuli*. Another area of the inner tympanic wall remains unchondrified, subsequently subdivided to form the *fenestra rotunda* (Fig. 240) and the *aqueductus cochleae*. In the 11th week a second cistern—the *scala tympani*—begins to form at the fenestra rotunda, growing along the side of the cochlear canal, opposite to the *scala vestibuli*, thus bringing that canal to lie between two perilymphatic spaces. The vestibular and tympanic extensions meet and fuse at the lip of the cochlear canal, at the end of the 3rd month, thus forming the *helicotrema*.

Ossification of the Petro-mastoid.—About the end of the 4th month, four ossific centres appear in the periotic capsule; one, the **pteroitic**, gives rise to the tegmen tympani which forms the roof of the antrum, tympanum, and Eustachian tube; the petro-squamous suture marks its outer edge; the hiatus Fallopii marks its junction with a second centre—the **opisthotic**. This centre forms the posterior or vestibular half of the petrous bone. The **pro-otic** forms the anterior or cochlear half; the mastoid part, which appears on the surface of the skull, is developed from the **epiotic** centre. While the greater part of the petro-mastoid is formed in a cartilaginous basis, the dense layers which form the immediate bony capsule of the labyrinth, the modiolus and lamina spiralis of the cochlea, are laid down by the lining membrane of the perilymphatic space.

The Mastoid.—The mastoid part of the petro-mastoid is flat at birth; about the 2nd year the mastoid process appears as a slight knob, and it gradually grows downwards to form a cephalic lever for the sterno-mastoid, splenius and trachelo-mastoid muscles. The period of its most active growth is marked by the eruption of the permanent teeth. In most mammals the mastoid grows out as a flat, wing-shaped process continuous with the occipital crest, and thus increases the basal area of the skull on which the neck muscles are inserted (Fig. 148). The post-auditory process of the squamosal forms a considerable part of the mastoid process; it reaches to the apex and forms the anterior border (Fig. 181, C). As the mastoid process grows the diploic spaces within it enlarge into air spaces. Those round the antrum come to open into it, but the more distal remain closed. These spaces occupy the whole of the mastoid part of the temporal, but they also extend forwards in the post-auditory process of the squamosal, and may spread backwards to the occipital. Three varieties of mastoids are recognized: (1) Dense processes in which the air cells are minute or absent (infantile type of Cheatle); (2) a type containing numerous large spaces (pneumatic); (3) an intermediate type with large cells round the antrum, and a few small ones near the surface. The third type is the commonest.

¹ See Geo. L. Streeter, *Contributions to Embryology*, 1918, vol. 7, p. 5.

The Floccular or Subarcuate Fossa.—At birth there is a fossa situated on the posterior aspect of the petro-mastoid. It is filled with a process of the dura mater in the human embryo, but in all except the highest primates it contains the paraflocculus (Fig. 90), a part of the cerebellum which is quite vestigial in man. The posterior semicircular canal surrounds the fossa. This is the condition in most mammals throughout life, but soon after birth the fossa becomes closed in man, merely a remnant being seen above and internal to the hiatus vestibuli in the bone of the adult.

Organ of Corti.¹—In Fig. 244 is given a diagrammatic section across the cochlear canal to show the manner in which its ectodermal lining is modified to form the organ of Corti—the machinery concerned in producing auditory stimuli. The canal has become three-sided—one side lying against the scala vestibuli (vestibular wall), another against the

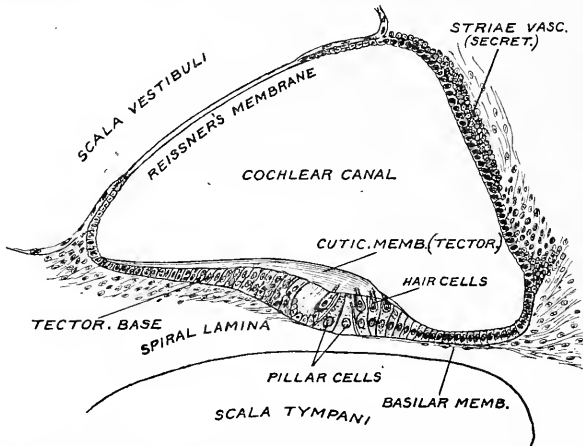


FIG. 244.—Diagrammatic section across the Cochlear Canal of a newly born child to show the differentiation of Ectodermal Epithelium to form the Organ of Corti. (After Keibel.)

scala tympani (tympanic wall), the third being peripheral or outer. The ectoderm on the vestibular wall atrophies and disappears—the fibrous base forming Reissner's membrane. The ectoderm is modified to form a secretory apparatus—the vascular body (striae vasculares). On the tympanic wall the ectoderm is modified to form, (a) hair or sensory cells, (b) supporting or pillar cells—comparable to neuroglial cells in the spinal cord, and fibres of Müller on the retina; (c) tectorial cells, producing a peculiar cuticular substance, which forms the tectorial membrane—in which the hair processes of the sensory cells are embedded. The auditory nerve fibres commence round the hair cells.

While in the saccule, utricle and ampullae of the semicircular canals, the hair cells are planted on a fixed base, their hair-like processes being moved by otoliths acting under the influence of gravity, or by currents set up in the semicircular canal, the hair cells of the cochlea are planted

¹ For differentiation of Organ of Corti see O. van der Stricht, *Contrib. to Embryology*, 1920, vol. 9, p. 109.

on a movable base—the basilar membrane, which responds to every movement of the stapes, because of the displacement of perilymph in the adjoining scalae. The tectorial membrane bends the hair-like processes with every movement of the basilar membrane, because the tectorial membrane is attached to a fixed base on the spiral bony lamina while the hair cells rest upon a movable one.

The Acoustic Ganglia.—The origin of the mass of nerve cells lying between the otocyst and hind-brain has already been mentioned (p. 224). It becomes divided into three parts: (1) the **geniculate ganglion** of the facial nerve, which is included in the petro-mastoid, but has no functional relationship to the labyrinth; it gives rise to the great superficial petrosal nerve, chorda tympani and pars intermedia (root part of ganglion) in the same manner as a ganglion of the posterior root produces the sensory

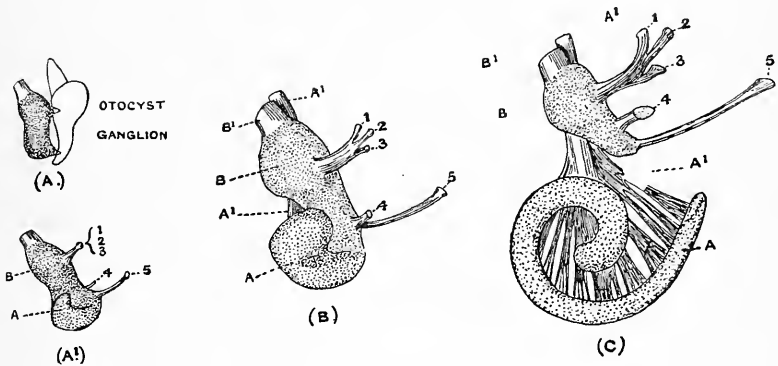


FIG. 245.—The differentiation of the Ganglion of the Labyrinth. (Streeter.)
 A. The otocyst and ganglion of a human embryo in the 4th week; A¹. In the 5th week. The parts are those of the left side, and are viewed on their lateral aspect. B. From a foetus in the 7th week (16 mm. long); C. From a foetus in the 9th week (30 mm. long).

- | | |
|--|-------------------------|
| 1. Branch from ampulla of superior canal. | 3. Branch from utricle. |
| 2. Branch from ampulla of lateral canal. | 4. Branch from saccule. |
| 5. Branch from ampulla of posterior canal. | |

A. Cochlear ganglion. A¹. Cochlear nerve.

fibres of a spinal nerve (Dixon) (Fig. 93); (2) the **vestibular** part—applied to the vestibular part of the labyrinth; (3) the **cochlear** part, which becomes applied to the cochlear canal (scala media). The differentiation of the vestibular and cochlear ganglionic masses proceeds at the same rate as the development of the membranous labyrinth.¹

In Fig. 245 four stages in the differentiation of the nerve equipment of the ear are reproduced. The figures are those of Professor Streeter² and represent stages in the first, second and third months of development. Towards the end of the first month the cochlear part becomes apparent (A¹); in the second month this part is undergoing rapid growth (B); early in the third month (C) it has assumed a spiral form, and lies within the spiral lamina of the cochlea, and hence is often named the spiral ganglion. The cells of the spiral ganglion send out two sets of processes—to the

¹ Cameron and Milligan, *Journ. Anat. and Physiol.* 1910, vol. 44, p. 111.

² *Amer. Journ. Anat.* 1907, vol. 6, p. 139.

organ of Corti (peripheral fibres), to ganglia situated in the hind-brain (root fibres). The cochlear fibres form the lateral root of the VIIIth nerve. The vestibular ganglionic mass becomes partially subdivided into a dorsal mass—connected with the areas of sensory cells in the utricle and the ampullae of the superior and external semicircular canals (Fig. 245, 1, 2, 3); the lower or ventral mass, which sends fibres to the saccule and posterior semicircular canal. The vestibular ganglion is lodged in the fundus of the internal auditory meatus. Its ingrowing or centripetal fibres form the mesial root of the VIIIth nerve. While the cochlear root enters the floor of the 4th ventricle superficial to the inferior peduncle of the cerebellum, the vestibular or mesial root passes deep to it. The lateral or cochlear root is connected with hearing, the mesial or vestibular with balancing.

Nerve Centres. (1) **Cochlear or auditory.**—By the end of the 5th week (Fig. 246) the ingrowing root fibres of the cochlear ganglion have

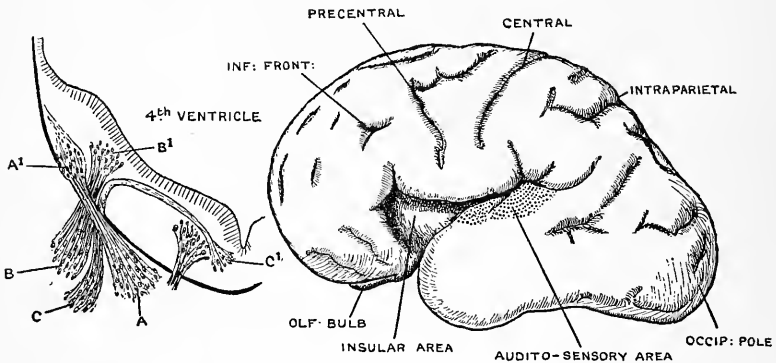


FIG. 246.—Section across on half of the Wall of the Hind-Brain of an Embryo at the end of the first month. (His.) *A*. Peripheral cochlear ganglion; *A'*. Central cochlear ganglion; *B*. Peripheral vestibular ganglion; *B'*. Central vestibular ganglion; *C*. Geniculate ganglion of facial; *C'*. Motor nucleus of facial nerve; the motor nucleus of the VIth cranial nerve is shown adjacent to that of the VIIth.

FIG. 247.—Lateral view of the Cerebrum of Foetus in the seventh month of development. (Retzius.) The audio-sensory area on Heschl's gyri is stippled.

reached a central mass of nerve cells (central cochlear mass) developed in the alar lamina of the hind-brain. The central cochlear ganglion gives rise to the acoustic tubercle (situated on the restiform body) and a lateral accessory nucleus on the outer aspect of the restiform body. By means of the striae acousticae and lateral fillet the cochlear central ganglia are united with the superior olive, inferior corpus quadrigeminum (mid-brain) and internal geniculate body (thalamencephalon) of the opposite side. Projection fibres connect the geniculate body with the cortex of the first temporal gyrus (see Fig. 113). Heschl's gyri (audio-sensory) of the first temporal convolution are already apparent at the beginning of the 7th month (see Fig. 247). The cortex of these gyri, with the neighbouring area of the first temporal, receives the fibres from the internal geniculate nucleus, and forms the audio-sensory areas. It is highly probable that the

cortex of the greater part of the temporal lobe forms association areas, for the interpretation of sounds. The auditory centres are necessarily connected with the centres for sight, movement and speech, but the development of these connections is as yet imperfectly known.

(2) The ingrowing fibres of the vestibular ganglion pass beneath the inferior peduncle of the cerebellum to terminate in the nerve cells of the dorsal nucleus and Deiter's nucleus in the floor of the 4th ventricle (Fig. 246). These nerve cells and fibres are in no sense auditory, but concerned with the balancing of the body. Through the inferior peduncle of the cerebellum, the nuclei in which the vestibular root ends are connected with both the vermis and lateral cerebellar lobes. The cerebellum and acoustic ganglia arise from the same part of the hind-brain; there is a close developmental relationship between the origin of the vestibular or balancing part of the ear and the cerebellum.

Internal Auditory Meatus.—The internal auditory meatus is formed round the 8th nerve, its ganglia, and the 7th nerve. The falciform crest separates the fibres of the dorsal and ventral parts of the vestibular nerve. The meatus also contains a prolongation of the arachnoid and subarachnoid space. Fractures of the base of the skull frequently cross the petro-mastoid in the line of the internal auditory meatus, vestibule and membrana tympani. In such cases the cerebro-spinal fluid and perilymph may escape by the external auditory meatus.

Summary.—A study of the development and evolution of the human ear leads to the following conclusions :

- (1) That the otocyst was originally an external sense organ connected with the balancing of the body; it became encysted above the first visceral cleft, and part of it became sensitive to sound waves.
- (2) Parts of the dorsal laminae of the hind-brain were connected with it, and from those were developed the acoustic ganglia and nuclei, and probably also the cerebellum (see page 85).
- (3) The first and part of the second clefts were modified in air-breathing forms, to become air passages for transmitting sounds.
- (4) Parts of the skeletal bases of the first and second visceral arches became the auditory ossicles.

CHAPTER XVII.

PHARYNX AND NECK.

IN previous chapters the origin of various pharyngeal structures has been touched on. We have seen that a forward prolongation of the archenteron during the 3rd week gives rise to the fore-gut (Fig. 18), that the anterior or pharyngeal part of the fore-gut is separated from the primitive mouth or stomodaeum by the oral plate (Fig. 102), that the notochord is laid down along the dorsal wall of the pharynx (Fig. 102) and that the heart lies under its floor, while the aortic arches encircle it (Fig. 80). Mention has been made of its cartilaginous skeleton (Fig. 150), of the segmentation of its mesoderm (Fig. 149) and of its nerves (Fig. 93). In this chapter we have to knit these isolated statements together by following the developmental changes which transform the simple fish-like pharynx of the embryo into the complex of structures found in the neck and throat of the adult.

Evolution of the Pharyngeal Region.—In the latter part of the first month and opening part of the second the neck of the human embryo undergoes a very remarkable transformation. In the 5th week, when the human embryo is about 5 mm. in length, representations of four gill clefts and five gill or branchial arches are plainly to be seen in the region of the neck or pharynx (Fig. 248); the elevation caused by the heart reaches forwards almost to the mandibular arch; properly speaking, there is no neck at the 4th week; as in a fish, the head is fixed directly to the body. By the beginning of the 7th week (Fig. 43, p. 46) all traces of the branchial arches have disappeared; the head of the embryo is now extended and lifted away from the thoracic region, which now contains the heart. Before the branchial arches have begun to disappear in the 6th week, a pouch has grown out from the floor of the pharynx to form the larynx, trachea, bronchi and lungs (Fig. 250). In the passage from the 6th to the 7th week of development we see the human embryo evolve from a stage in which the parts are adapted for a branchial respiration, as in fishes, to a higher one in which its parts are fitted for breathing air. Pharyngeal glands, such as the tonsil, thyroid and thymus, originally developed in connection with the visceral or gill arches, become modified in structure and position to suit the new conditions of life. With the evolution of the mammalian method of mastication and swallowing, the pharynx, originally a respiratory structure, was further modified. The tongue became differentiated from parts in the floor of the pharynx, and muscles, which were at first

designed to move the branchial arches, became converted into muscles of deglutition.

Pharynx of the Embryo.—There is very little resemblance between the pharynx and neck of a human embryo in the third week and that of the

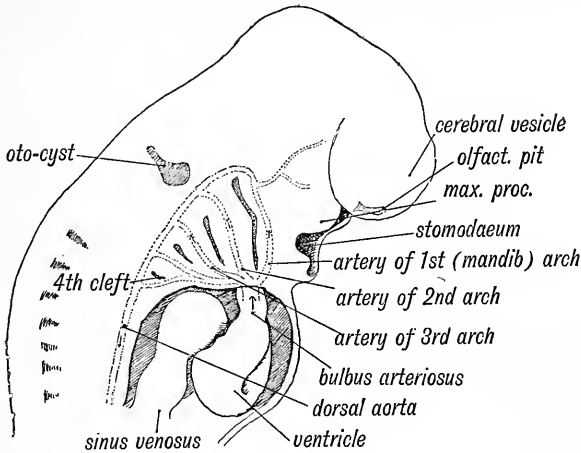


FIG. 248.—Showing the Visceral Arches and Cleft-depressions in the Pharyngeal Wall of a Human Embryo at the beginning of the 5th week. Each Visceral Arch contains an Aortic Arch. (After His.)

adult. Indeed, in the 4th week the human pharynx resembles closely that of a fish (Figs. 248, 249). In both the human embryo and fish the pharynx is bounded by **visceral** or **branchial arches**, which are separated by depres-

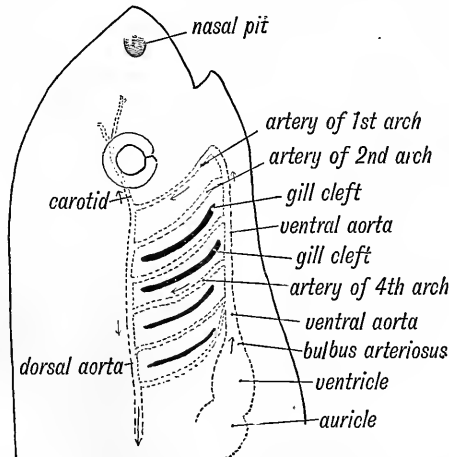


FIG. 249.—Showing the position of the Heart, Visceral and Aortic Arches in a Fish. (Diagrammatic—after Gegenbaur.)

sions (human embryos) or clefts (fishes); in both the heart is situated under the pharynx, and from the ventral aorta, aortic arches pass up on each side, one in each visceral arch, to terminate in the dorsal aortae. In fishes the

aortic arches give off vessels to the gills, in which the blood is arterialized. In the human embryo the blood passes directly through the aortic arches. The walls of the pharynx were, therefore, primarily respiratory in function.

A considerable part of the human neck lying in front of the vertebral column and between the mouth above and the thorax and clavicles below, with the bounding walls of the adult pharynx, is formed from the embryonic visceral arches. A knowledge of the transformation of the embryonic to the adult pharynx is of the utmost practical importance: it explains the occurrence of fistulae and cysts found in the neck;

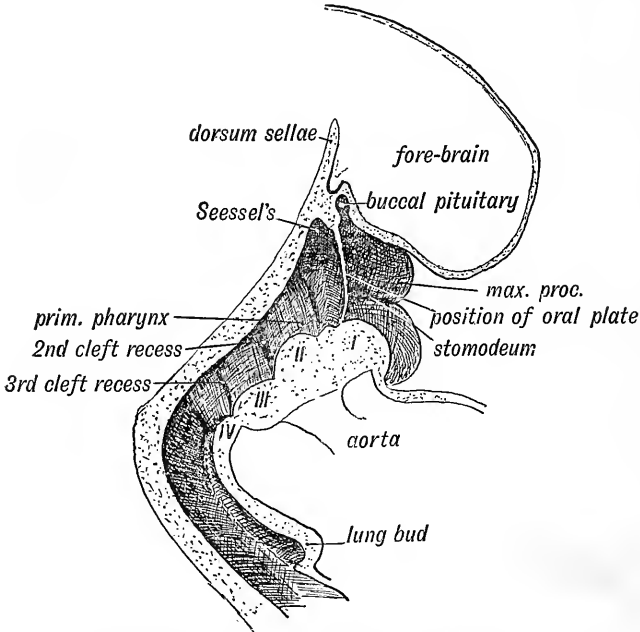


FIG. 250.—Showing the Primitive Pharynx of a 5th week Embryo in Sagittal Section, bounded by the Visceral Arches. (After His.)

it accounts for the peculiar courses taken by nerves, such as the recurrent laryngeal and phrenic; it explains the peculiar distribution of nerves to the pharynx; and throws light on the nature and anomalies of the thymus, thyroid and tonsil. As may be seen from Fig. 248, the floor of the pharynx of the human embryo rests on the dorsal wall of the pericardium; in the adult the pharynx and pericardium are separated by the whole length of the neck.

Visceral Arches.—The visceral arches bound and form the whole thickness of the wall of the primitive pharynx, which is flattened dorso-ventrally, so that its cavity forms a transverse cleft when seen in cross-sections of the embryo. Four arches, each bounded behind by a depression, are to be recognized superficially on each side of the pharynx of the 5th week human

embryo (Fig. 248), but behind the 4th cleft are fifth and sixth arches which, however, never become raised or superficially differentiated from the body wall behind (Fig. 251). Sagittal and coronal sections of the primitive pharynx (Figs. 250 and 251) give a better idea of the arrangement and constitution of the visceral arches than can be had from a surface view. They are developed round the most anterior part of the fore-gut, which forms the lining membrane of the primitive pharynx. The pharyngeal lining membrane, therefore, is the same as that of the alimentary canal from which spring all the organs and glands of digestion and assimilation.

Visceral Clefts.—The epithelium or entoderm, which lines the primitive pharynx, covers the inner aspects of the arches and passes outwards in the recesses between them and there, for a short time, comes in contact with the epithelial covering of the body (ectoderm) which dips in to meet it

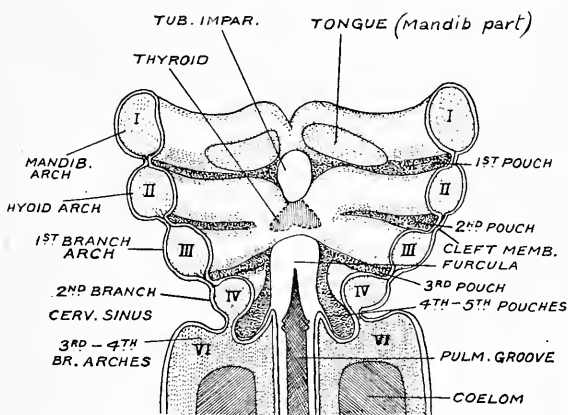


FIG. 251.—Showing the Floor of the Pharynx of a 5th week Human Embryo. (After His.)

(Fig. 251). The membrane thus formed by the union of the ectoderm and entoderm in the recesses between the arches, may be named the "cleft membrane." It is never ruptured nor disappears in the development of mammals, but is invaded by the mesoderm of neighbouring arches; in fishes it disappears and real clefts are formed between the arches. On the outer side of the membrane is the "cleft depression," on its inner side a "pharyngeal recess," presently developed into a pouch. From the entodermal lining of the pharyngeal pouches we shall see that the tonsil, thyroid and thymus arise: from the external depressions are formed the various branchial cysts and fistulae, which occasionally occur in the neck of the adult. Further, at the upper end of each cleft depression there develop remarkable sense-organs, known as the *epibranchial placodes*. In each arch there develop exactly the same elements as are to be seen in the gill arches of fishes, namely:

(a) A skeletal basis of **cartilage**; (b) an **aortic or vascular arch**; (c) a **larger nerve** along its anterior border and a **smaller** along its posterior; (d) a **muscle element**.

In Fig. 149 (p. 155) a schematic transverse section of a vertebrate embryo has already been given to show the relationship of the tissues of a branchial arch or branchiomere to the segments of the head.

The first visceral arch is known as the mandibular, the second as the hyoid (Fig. 251). The remaining four are **branchial** arches, having been at one stage of evolution devoted solely to the purpose of carrying gills. The hyoid arch is specialized in fishes, to protect the branchial arches, and assist in the circulation of blood through the gills and water through the pharynx. The mandibular arch bounds part of the buccal cavity in all vertebrates, and forms part of the apparatus of mastication.

Formation of the Cervical Sinus.—The first arch especially, and also the second, grow and increase at a much greater rate than the branchial

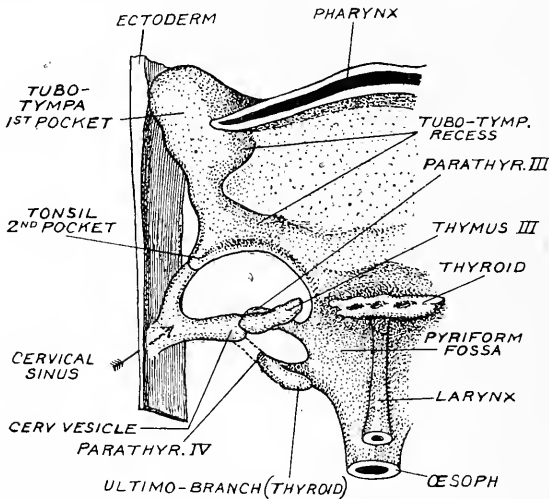


FIG. 252.—The Lining Membrane of the Pharynx of a Human Embryo at the end of the 6th week of development (10 mm.) viewed on its ventral aspect. (Grosser.)

arches. The second arch (hyoid) which in fishes forms the operculum for the gills, grows over and buries the third and fourth in the human embryo. Already at the end of the 5th week (Fig. 251) there is clear evidence of the sinking in of the hinder arches, and it is easy to see that as the hyoid arch grows backwards over them, an ectodermal space will become covered over and form the cervical sinus—representing the gill cavity of fishes. Its formation is effected in the 6th week. In Fig. 252 a model of the lining membrane of an embryo at the end of the 6th week of development is depicted as seen on its ventral aspect. The enclosed pocket of ectoderm—the cervical sinus—is shown to be connected with the 3rd pouch by a vesicular prolongation—the *cervical vesicle*, also by extensions to the 2nd or tonsillar pouch and to the 4th. The last named connection is short lived; indeed, before the end of the 2nd month all traces of the sinus should have disappeared.

Although the cervical sinus usually disappears, it may remain and form a cyst in the neck, which opens on the anterior border of the sterno-mastoid a short distance above the sterno-clavicular joint. It may be drawn out into a trumpet-shaped tube, which ends in contact with the tonsillar recess, passing between the internal and external carotid arteries or in contact with the pharynx behind the hyoid (Fig. 253), connections which are explained by the origin of the sinus (Fig. 252). Often the cutaneous orifice is marked by a tag of skin representing a rudimentary external ear, which encloses a piece of cartilage.¹ If the outer cleft depression in front of or behind the third arch persist, it must open in the cervical sinus.

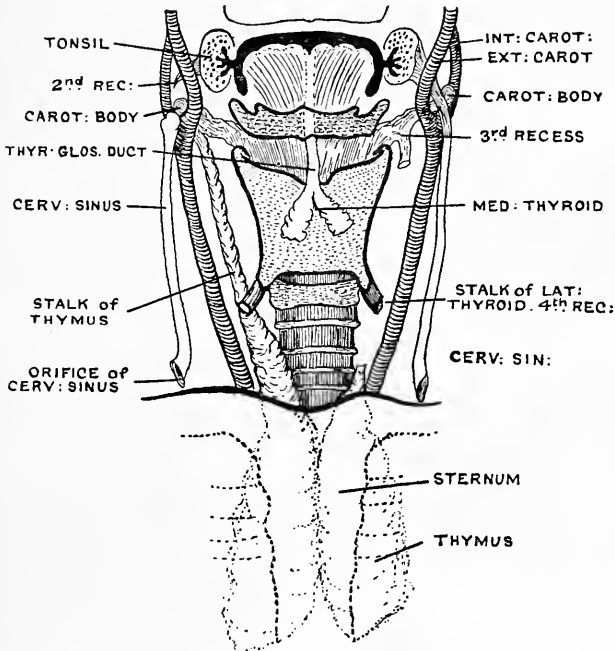


FIG. 253.—Diagram to illustrate the various parts of the Visceral Clefts which may persist. The 2nd inner cleft recess gives rise to the tonsil; the recess may be in contact with an epithelial tube derived from the cervical sinus. The 3rd inner recess gives rise to the thymus and carotid bodies.

What becomes of the Visceral Clefts.—By the end of the second month the clefts, or, to be more exact, the representatives of clefts in the human embryo, have disappeared, except the upper part of the first. From the external depression of this part a solid ingrowth of epithelium takes place which, ultimately becoming canaliculized, forms the **external auditory meatus** (Fig. 230). In connection with the upper or dorsal parts of the first and second cleft depressions the **Eustachian tube** and **tympa-**

¹ For an account of the various developmental anomalies of the pharyngeal region see Keith, *Brit. Med. Journ.* 1909, Aug. 7th, 14th, 21st. For a description of its development see J. Ernest Frazer, *Journ. Anat. and Physiol.* 1910, vol. 44, p. 156; H. Fox, *Amer. Journ. Anat.* 1908, vol. 8, p. 187; B. Kingsbury, *Amer. Journ. Anat.* 1915, vol. 18, p. 329.

are formed, the **membrana tympani** remaining approximately in the position of a cleft membrane (p. 232).

If traces of the other clefts remain as fistulae or cysts they will occur in the positions shown in Fig. 254. Part of the second cleft is marked in the goat by an opening and auricular appendage. As already pointed out, superficial remnants of the second and third clefts are rare; they are usually included with the cervical sinus beneath the hyoid operculum.

Within the pharynx traces of inner cleft recesses are to be seen besides the Eustachian opening (see Figs. 253, 266). The **tonsil** is developed in the second cleft; the anterior pillar of the fauces represents only the

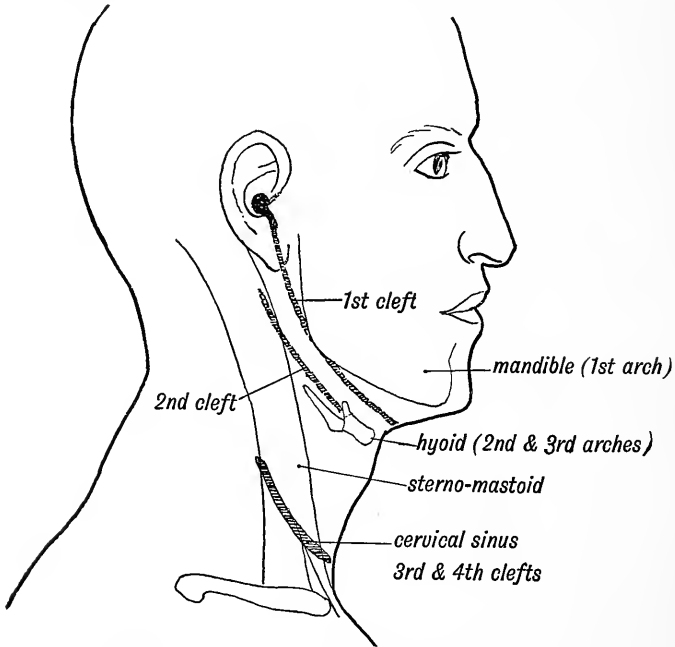


FIG. 254.—Showing the position of the External Cleft Depressions in the Adult.
(For explanation, see text.)

position of the second arch. The **lateral recess of the pharynx** (fossa of Rosenmüller), behind the Eustachian tube, although sometimes regarded as a derivative of the second cleft, is, as we have seen (p. 228), a secondary formation. The **pyriform fossa**, at each side of the laryngeal aperture, represents the position of the fourth and fifth clefts (see Fig. 253).

The Cartilages of the Arches (Fig. 255).—The history of the skeletal basis of the first arch (Meckel's cartilage) has been already traced (p. 175).

The cartilage of the 2nd or **hyoid arch** forms (Fig. 255):

(1) The **tympano-hyal**, embedded in the petro-mastoid, and originally continuous with the ear ossicles (Fig. 237). (2) The **stylo-hyal**, which ossifies in the early years of life and becomes joined to the tympano-hyal to form the styloid process. (3) The segment below, the **epi-hyal**, becomes

ligamentous, and forms the stylo-hyoid ligament, but it also may become ossified. (4) The lowest segment, the **cerato-hyal**, forming the small horn of the hyoid. The **epi-hyal** lies behind and outside the tonsil, and when ossified has been excised under the belief that it was a foreign body. The body of the hyoid (**basi-hyal**) represents the fused ventral parts (copulae) of the **2nd and 3rd cartilages**; in the floor of the embryonic pharynx (Fig. 251) the ventral ends of the 2nd and 3rd arches end in a common or mesobranchial field. In this area the body of the hyoid develops.

Prof. Parsons¹ has drawn attention to the fact that there is a ridge of bone on the upper surface of the body of the hyoid, which may occasionally form an almost separate bar. It lies between the lesser horns, and appears to represent the copula or body of the 2nd arch. It may be separated

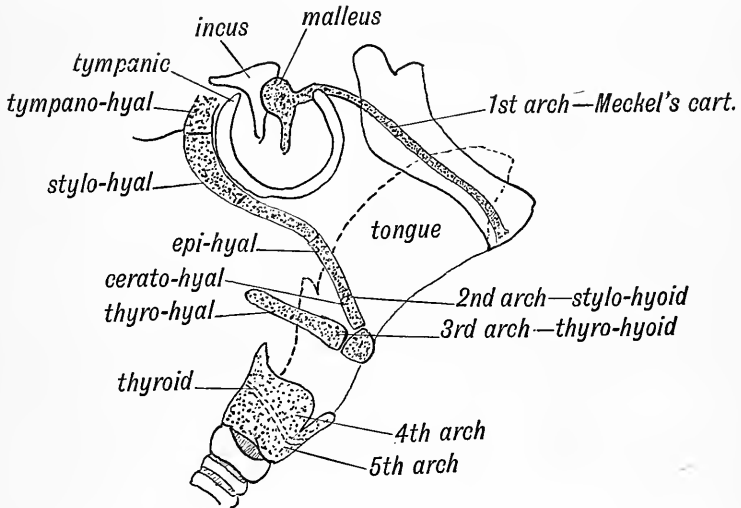


FIG. 255.—Showing what becomes of the Cartilages of the Visceral Arches.

from the body of the hyoid by a foramen evidently for the passage of a remnant of the thyro-glossal duct. It will be seen later that the basal or pharyngeal part of the tongue arises from the floor of the pharynx in the field between the 2nd and 3rd arches. The skeletal bases of their ventral parts come to form the bone of the tongue. The skeletal part of the hyoid arch suspends the tongue. There may be a process of bone from the concavity of the body representing the hyolingual of lower vertebrates (Parsons).

The **great horn** of the hyoid represents the cartilage of the **3rd arch** (Fig. 255). In the lowest mammals the cartilaginous bases of the 4th and 5th arches unite to form the thyroid cartilage, but in higher mammals, including man, this cartilage is made up entirely by the 4th arch.² The cartilages of the ultimate arches (5th and 6th) are probably represented by the cricoid, arytenoid and rings of the trachea (see also Fig. 375, p. 352).

¹ F. G. Parsons, *Journ. Anat. and Physiol.* 1909, vol. 43, p. 279.

² F. H. Edgeworth, *Quart. Journ. Mic. Sc.* 1916, vol. 61, p. 383.

Even in mammals the cartilages of the three last branchial arches remain subservient to the purposes of respiration, just as in vertebrate animals in which these arches carry gills.

Nerves of the Visceral Arches (see Figs. 256, 257, 93).—The 3rd division of the 5th nerve is, as has been already seen, the principal nerve of the first or mandibular arch. The nerve for the second or hyoid arch is represented by the 6th or facial. The nerve of the 3rd arch is the glosso-pharyngeal, that for the 4th is the superior laryngeal branch of the vagus, and for the 5th and 6th the inferior laryngeal (Fig. 257).

Each nerve of a visceral arch supplies (1) the muscles of the arch, (2) the pharyngeal lining and cleft recess in front of the arch. The chorda

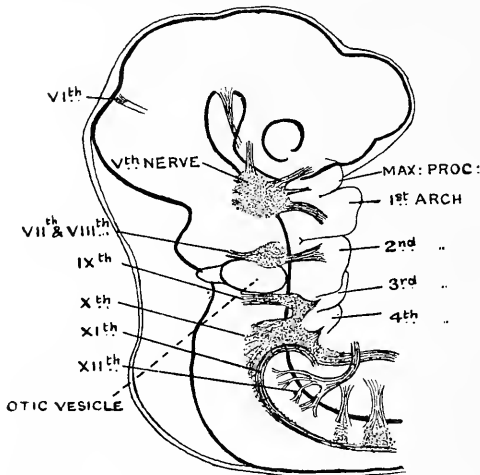


FIG. 256.—The Visceral Arches and their Nerves and Ganglia in a Human Embryo of the 5th week. (Professor Streeter.)

tympani and great superficial petrosal nerves represent the sensory branches of the facial to the first cleft.

The relationship of the nerves to the visceral arches is shown in Fig. 256, in a human embryo of five weeks. The position of these nerves in the adult is diagrammatically represented in Fig. 257. The Vth nerve and Gasserian ganglion are seen to lie at the base of the mandibular process. The ganglion of the VIIth and VIIIth nerves lies at the base of the hyoid (second) arch, in front of the otic vesicle, the fibres of the facial having already entered the arch. The glosso-pharyngeal and its ganglia lie behind the otic vesicle and at the base of the third arch. The large ganglionic mass of the vagus lies over the bases of the fourth, fifth and sixth arches—or rather the tissue representing these arches. At this stage—the 5th week—the ganglion of the vagus and its issuing fibres rest on the dorsal wall of the pericardium, the heart being quite close to the source of its nerve fibres.

Epibranchial Placodes.—When the ganglia of the VIIth, IXth and Xth nerves begin to differentiate in the 5th week, they are in contact with

the upper ends of their respective gill depressions—the 1st, 2nd and 3rd. An area of ectoderm at the upper end of each cleft depression becomes modified to form an *epibranchial placode* representing sense organs which are now lost in higher vertebrates. During the 5th week these placodes are in contact with the ganglia just mentioned and the ganglion of the trunk of the vagus (ganglion nodosum) and of the trunk of the glosso-pharyngeal (ganglion petrosum) receive additions from cells which are produced in, and migrate from, the placodes.

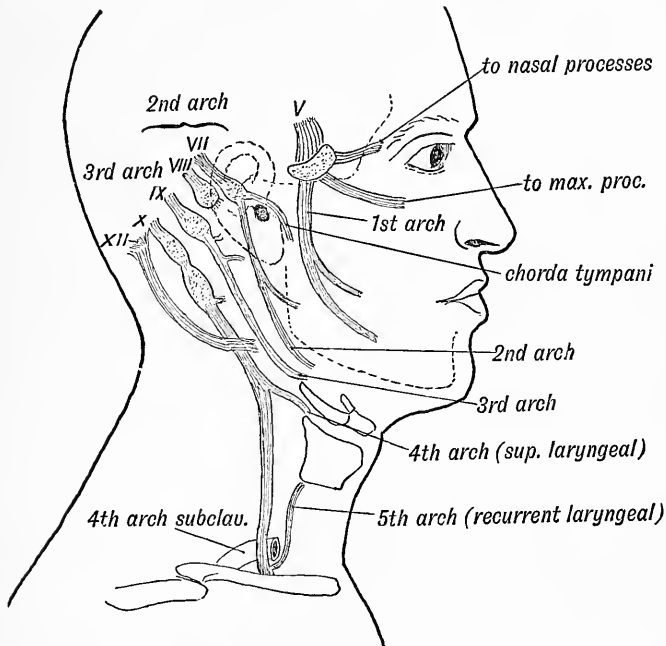


FIG. 257.—Showing what becomes of the Nerves of the Visceral Arches.

Aortic Arches—the Arteries of the Visceral Arches.—In Fig. 248 is given the foetal arrangement of the aortic arches, and in Fig. 258 the vessels in the adult which are formed from them. The primitive aorta in the embryo divides into two trunks, which run forwards along the floor of the pharynx, one on each side, lying between the ventral ends of the visceral arches. These may be termed the right and left **ventral aortic stems**. From these stems arteries (aortic arches) pass upwards, one in each visceral arch, to terminate in the right and left **dorsal aortae**, which run backwards and become fused to form the descending thoracic aorta. The aortic arches are formed at a very early date. At the beginning of the 4th week the first or mandibular aortic arch is already present; the second (hyoid), third, fourth, fifth and sixth appear in succession, but by the 6th week, when the 6th or pulmonary arch¹ has appeared, the first

¹ For literature on 6th arch and 5th cleft recess see Frank Reagan, *Amer. Journ. Anat.* 1911, vol. 12, p. 493; J. Tandler, *Anat. Hefte*, 1909, vol. 38, p. 393.

and second are in a process of atrophy. Only for a brief period towards the end of the 5th week, when the embryo is about 5 mm. long, are all the arches open, and even then the 1st is atrophic while the 6th or pulmonary is developing. The 5th arch has only a transient existence. The aortic arches are formed by the union of a network of blood spaces which are developed within each visceral arch.

The 1st and 2nd aortic arches disappear; the 3rd remains as the first part of the internal carotid, the 4th forms the 1st and 2nd stages of the

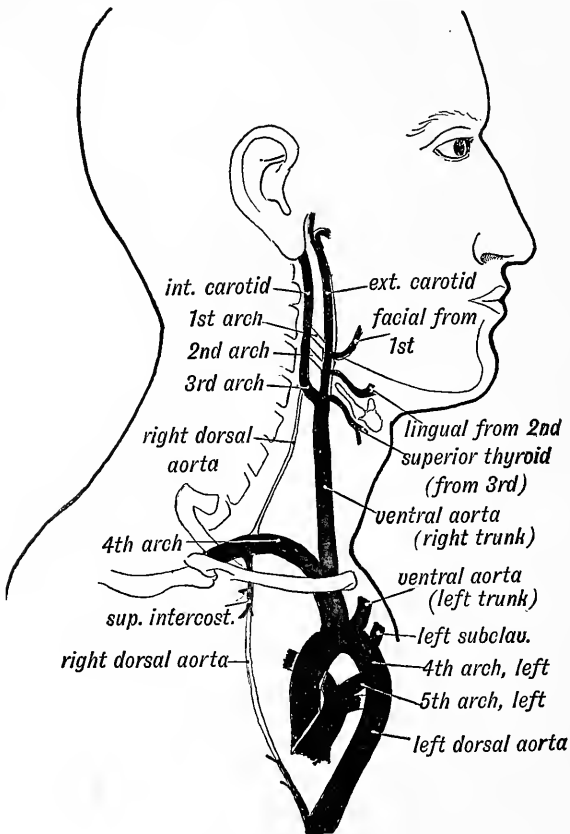


FIG. 258.—Showing what becomes of the Aortic Arches in the Adult. Only the shaded parts persist. The position of the 1st and 2nd aortic arches should be indicated above and below the position of the external auditory meatus.

right subclavian. On the left side the 4th aortic arch forms that part of the arch of the aorta between the origin of the left carotid and entrance of the ductus arteriosus (Fig. 258). The right and left 5th arch, or, to be more accurate, the 6th, for a transient arch appears between it and the 4th, give off vessels to the lungs which are developed in close connection with these arches. This arch on the left side persists as part of the right pulmonary artery and ductus arteriosus (Fig. 260). On the right side

the dorsal part disappears, the remaining segment joining in the formation of the right pulmonary artery. When it is remembered that the 6th or pulmonary arch lies at the level of the larynx in the 5th week, and that, owing to the development of the neck, it has almost reached its final position in the 7th week, the rapid transformation of the parts in the region of the pharynx in the second month will be realized. It is in this period that the hinder gill arches are buried and the cervical sinus formed and obliterated.

Subclavian Arteries.—The visceral arches with their arteries are well developed before the limb buds appear. When, at the end of the 4th week, these buds grow out to form the upper extremities, the artery which supplies each bud springs from the dorsal aorta and represents a dorsal segmental branch of that vessel. The embryonic or primitive subclavian

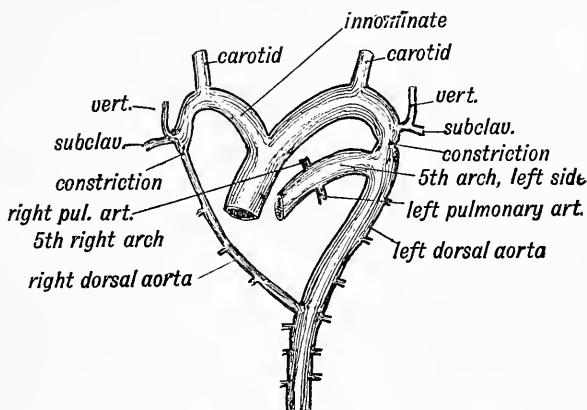


FIG. 259.—The condition of the Right and Left Dorsal Aortae in a 7th week Human Foetus. (After His.) The right arch and right dorsal aorta disappear beyond the origin of the right subclavian; a constriction may appear at the corresponding point on the left side.

is the artery of the 7th cervical segment, being situated at a considerable distance behind the 6th aortic arch. As the aortic arch-system is elongated to form the great vessels of the neck during the 6th and 7th weeks, the origin of the subclavian comes to lie opposite the 4th arch (Fig. 259). This artery forms the entire subclavian on the left side, but only that part beyond the origin of the vertebral on the right side (Fig. 259).

Aortic Arch on the Right Side.—In birds it is the 4th right arch which forms the aortic arch, and this occasionally happens in man. In amphibians both the right and left 4th arches persist. The two dorsal aortae in which they end, unite together, as they do in the human embryo, to form the descending thoracic aorta. The primitive subclavian arteries spring from the dorsal aortae above the point where these two vessels fuse together. In the latter part of the second month the short part of the right dorsal aorta, between the origin of the right subclavian artery and point of aortic fusion, disappears, and then the subclavian artery appears as if it arose from the 4th right arch (Fig. 259). The communicating

arterial twig, which is often seen uniting the superior intercostal artery of the right side with the artery of the lower spaces, is formed by a secondary anastomoses, and does not represent the right dorsal aorta.¹

Not unfrequently the right subclavian arises, not from the innominate, which represents the right ventral aortic stem, but as the last of the great branches which arise from the arch of the aorta (Fig. 260). In such cases two things have happened: (1) the 4th right aortic arch has been obliterated, (2) the right dorsal aorta has persisted.

Cases occur in which the permanent aorta is very much constricted at or near the point of entrance of the ductus arteriosus (see Fig. 259). It will be noticed that the corresponding part of the right dorsal aorta is obliterated. Such a constriction on the left side is to be regarded as corresponding to that on the right side, and indicates an attempt to produce a right aortic arch.

Dorsal Aortae.—It will be noticed that the parts of the dorsal aortae between the 3rd and 4th arches disappear (Fig. 260). The ventral aortae persist as the innominate, the common carotid and external carotid arteries. With the marked elongation of the cervical region and the development of the lungs in the second month, the primitive position of the aortic arches is greatly disturbed. The heart, being the pump of the lungs, must accompany these organs. The ventral aortae become elongated into the common

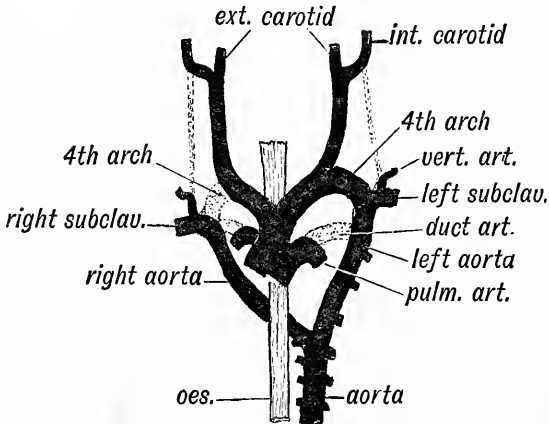


FIG. 260.—Diagram showing the manner in which the Right Subclavian may arise as the last branch of the Arch of the Aorta. The parts of the aortic arch system which become obliterated are stippled.

carotid and innominate arteries (Figs. 258, 260). The 4th aortic arch, which should lie opposite the upper part of the thyroid cartilage, comes to rest at the level of the 1st rib on the right side and within the thorax on the left, while the last aortic arch dragging the nerve of its segment in front of it (the recurrent laryngeal) comes to be situated within the thorax.

¹ See E. Pearce Gould, *Journ. Anat. and Physiol.*, 1909, vol. 43, p. 329.

Muscles of the Visceral Arches.¹—Within each visceral arch a muscle plate is formed—recalling in mode of appearance the muscle plates which develop in connection with each vertebral somite. The muscles arising in each arch are supplied by the nerve of that arch; hence from the nerve supply alone one could infer the derivation of the musculature of the pharyngeal region. The muscles become differentiated in the latter part of the second month. All the muscles supplied by the facial nerve—the platysma, muscles of expression, the stapedius, stylo-hyoid, posterior belly of the digastric, etc.—are derived from the muscle plate of the 2nd or hyoid arch. The muscles of mastication, with the tensors of the palate and tympanum, the anterior belly of the digastric and mylohyoid, are derived from the muscle segment of the mandibular arch. The stylo-pharyngeus is derived from the 3rd arch. The musculature of the soft palate and the constrictors of the pharynx are derived from the third and fourth arches. The musculature of the larynx comes from the fifth and sixth arches.

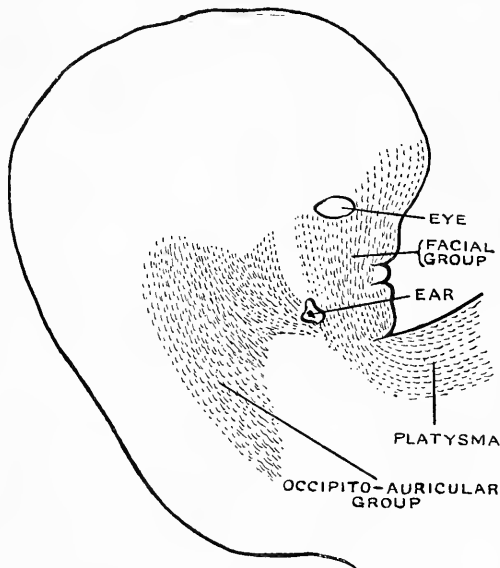


FIG. 261.—The expansion of the Platysma Sheet in a Human Foetus of 7 weeks. (Futamura.)

The Platysma and Muscles of the Face and Scalp.²—The platysma myoides, the muscles of the face, scalp and external ear, are derived from the muscle plate of the second or hyoid arch. They are supplied by the facial, the nerve of this arch. The muscle bud, from which the whole platysma sheet is developed, is still confined to the area of the hyoid arch until the 7th week of development when the bud spreads out and forms a continuous muscular hood over the head and neck. To this hood or sheet,

¹ F. H. Edgeworth, *Journ. Anat.* 1920, vol. 54, pp. 79, 124.

² R. Futamura, *Anat. Hefte*, 1907, vol. 32, p. 479; 1906, vol. 30, p. 433.

which is composed of two layers, a deep and superficial, the name of **platysma sheet** may be given. It is developed in the superficial fascia. During its expansion or migration the platysma sheet separates into three main divisions—a part for the neck—*platysma colli*; for the ear and occiput—the occipito-auricular; and the facial division—for mouth, nose, orbits and forehead (Fig. 261). The muscles become differentiated during the 3rd month.

In man, the platysma sheet has undergone marked retrograde changes in the neck, scalp and external ear, but over the face it has become more highly specialized and differentiated than in any other animal. From this sheet are derived the epicranial aponeurosis, the occipitalis and frontalis muscles. On the face the platysma sheet forms the muscles round the orbit, nose and mouth. The buccinator and levator anguli oris represent parts of the deeper layer of the sheet. The transversus nuchae, fibres occasionally seen in man passing from the middle line of the neck behind, towards the ear and cheek, represent fibres constantly developed in lower primates, and better still in rodents and carnivora as the *sphincter colli* and *sterno-facialis*.

The muscles supplied by the facial nerve are peculiar in that they are the physical basis into which many mental states are reflected and in which they are realized. Through them mental conditions are manifested. It is found that the differentiation of this sheet into well-marked and separate muscles proceeds *pari passu* with the development of the brain. The more highly convoluted the brain of any primate, the more highly specialized are its facial muscles. It is remarkable that the sheet should arise from a visceral arch, which originally was closely connected with the function of respiration. To some extent the platysma does come into play during forced respiration even in man.

The Neck.—If the reader will turn to Fig. 43 it will be seen that the head becomes demarcated from the trunk and a neck comes into existence in the human embryo during the 7th and 8th weeks of development. It is during these weeks that the fish-like organization of the embryonic pharynx becomes replaced by one which is mammalian. Although the seven cervical somites are demarcated early in the 4th week of development, the head is so flexed upon the trunk that the mandible is in contact with the pericardium. The neck comes into existence by the production and growth of tissues between the mandibular arch and pericardium, this growth in the ventral aspect of the cervical region being accompanied by an extension or elevation of the head. The heart itself is anchored to the roots of the developing lungs; all the tissues—nerves, vessels, muscles, air and food passages—passing from the head to the region of the thorax are elongated during this movement.

CHAPTER XVIII.

TONGUE, THYROID AND STRUCTURES DEVELOPED FROM THE WALLS OF THE PRIMITIVE PHARYNX.

The Tongue and its Development.¹—Two parts are to be recognized in the tongue. The **buccal part** (Fig. 262) is situated in front of the foramen caecum and the V-shaped groove. It is covered by papillae, concerned in mastication and liable to cancer. The second or **pharyngeal part**, bounding the buccal wall of the pharynx (Fig. 262), is covered by glandular and

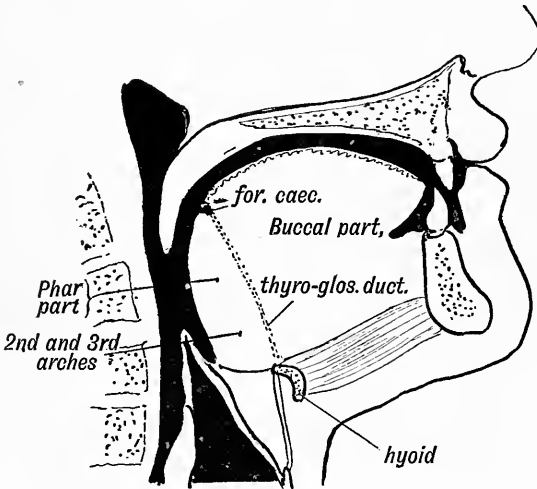


FIG. 262.—Showing the Buccal and Pharyngeal parts of the Tongue.

lymphoid tissue and concerned with swallowing. These two parts are not only different in function but also in origin and development.

The **buccal part** arises during the 4th week by an upgrowth—the *tuberculum impar*—which springs from the floor of the pharynx, in front of the united ventral ends of the 2nd and 3rd arches (see Figs. 251, 264). This outgrowth was at one time believed to give rise to the whole of the buccal part of the tongue, but researches made by Kallius and others have clearly demonstrated that in the 5th week there arise from the mandibular arch,

¹ E. Kallius, *Anat. Hefte*, 1910, vol. 41, p. 177, etc. ; J. L. Paulet, *Archiv. f. mikro. Anat. u. Entwickl.* 1911, vol. 76, p. 658 ; also reference on p. 226, under Frazer.

on each side of the tuberculum impar, right and left lingual buds which fuse with and bury the median element (Fig. 251). It is probable that this fusion has already occurred in Fig. 264, and that the tuberculum impar already represents the buccal element. Hence the buccal part of the tongue is bilateral in origin, and as its nerve supply shows, is entirely derived from the mandibular arch. In the 7th week the tip of the tongue is bifid, because the lateral buds are imperfectly fused (Paultet). The bilateral origin of the tongue explains the occasional occurrence of a bifid tip and the formation of cysts in the median raphe. Besides the lingual nerve, the chorda-tympani—the branch of the facial nerve which enters the mandibular arch—also supplies the buccal parts with sensory fibres. Until the 7th week the buccal part of the tongue, still separated from

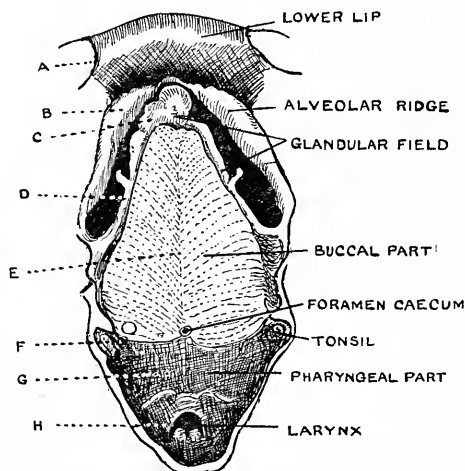


FIG. 263.—Upper Surface of the Tongue of a Child in which the glandular tissue, which forms the sublingual and submaxillary glands, has been imperfectly separated from the tongue by the down-growth of the mandibulo-lingual plate of epithelium. *A*, lower lip; *B*, alveolar ridge; *C*, glandular tissue (sublingual); *D*, submaxillary; *E*, buccal part of tongue; *F*, tonsil; *G*, pharyngeal part of tongue; *H*, opening of larynx.

the pharyngeal part by a depression in the floor of the pharynx, from which the thyroid bud has arisen, remains unseparated from the mandibular arch. There then occurs a down-growth of epithelium in the form of a horse-shoe plate, which separates the lingual from the mandibular tissues; in this way the tongue becomes separated from the alveolar ridge of the mandible. In the floor space between the tongue and mandible are developed the submaxillary and sublingual glands. Not unfrequently part of this glandular field may be imperfectly separated from the tongue, and in this manner various peculiar congenital malformations of the tongue are produced (see Fig. 263).

The **pharyngeal part** of the tongue is derived from the fused ventral ends of the 2nd and 3rd arches, in which, as we have already seen, the body of the hyoid is developed. The glosso-pharyngeal, the nerve of the 3rd arch, or more strictly of the 2nd cleft, supplies it. The V-shaped

groove (*sulcus terminalis*) marks the union of the buccal with the basal or pharyngeal part. The foramen caecum, at the apex of the V-shaped fissure, marks the site from which the thyroid outgrowth took place.

Musculature of the Tongue.¹—The muscles of the tongue, which make up almost its entire substance, do not arise within the visceral arches, but are of extraneous origin. It has been shown that the head is probably composed of nine segments. From the muscle plates of the three posterior or occipital segments processes arise and grow downwards and forwards until they reach the mesenchymal basis of the tongue derived from the three visceral arches, carrying their nerves with them—the hypoglossal or 12th cranial nerve (Fig. 257). Hence, while the sensory nerves of the tongue come from the nerves of the 1st, 2nd, and 3rd visceral arches, its motor fibres are derived from the posterior cephalic segments. The

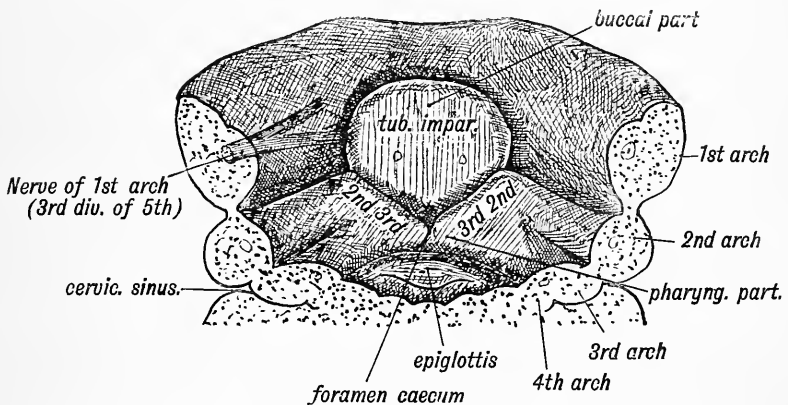


FIG. 264.—Showing the Origin of the Tongue in the Floor of the Primitive Pharynx. The condition represented is from an embryo in the 6th week. (After His.)

primitive muscle of the tongue is the genio-hyoid; the genio-glossus is a derivative of it, and so is the hyo-glossus. The lingual muscles are already recognizable in the 6th week, but the intrinsic muscles of the tongue, which have much to do with its fine movements, are later in point of differentiation—appearing in the fourth month. The sense of taste is present in a child born at the 8th month of development.

Lingual Papillae.—The filiform papillae are the first to appear, then the fungiform, a few of which, along the posterior border of the buccal part, become enlarged and sink to form circumvallate papillae, round the bases of which taste buds are developed. The papillae are confined to the buccal or masticatory part of the tongue. It will be observed that the taste papillae are situated at the brink of the pharynx (Fig. 262), at which the food is seized and carried away by the involuntary muscles. At the lateral margins of the buccal part of the tongue, just in front of the anterior pillars of the fauces, the fungiform papillae are arranged in a series of laminae, recalling and corresponding to the *papillae foliatae* of low primates

¹ See Warren H. Lewis, *Keibel and Mall's Manual of Human Embryology*, 1910, vol. 1, p. 518.

and of rodents. Between the papillae foliatae occur taste buds. On the under surface of the tongue at birth, on each side of the sublingual papillae and over the position of the ranine artery, are two fimbriated folds of mucous membrane, the **plicae fimbriatae**, structures which are well developed in lemurs, serving as tooth-combs¹ (Wood Jones). A remnant of the plicae fimbriatae can commonly be seen on the under surface of the human tongue.

The Epiglottis.²—The origin of the larynx, trachea, bronchi and lungs as a depression and bud from the floor of the pharynx will be dealt with later (p. 270); but the origin at the 4th week of the furcula (Fig. 251), a process from which the epiglottis is derived, may be noted here. Both epiglottis and thyroid cartilage arise from the 4th visceral arch. The superior laryngeal is the nerve of the 4th arch, hence it supplies the epiglottis and upper part of the larynx.

The epiglottis and palate are peculiar to mammals. They separate the respiratory passage from the mouth. In all mammals the epiglottis lies within the naso-pharynx in contact with the soft palate, but with the acquisition of speech in man this relationship is lost.

Origin of the Salivary Glands.³—In the depression between the tongue and the mandible, formed by the opening out of the linguo-mandibular plate of epithelium, there appear two linear furrows (Fig. 265). From the inner or mesial of these two furrows arises the submaxillary gland; from the outer or lateral, at a rather later date (7th week), grows the sublingual. While the latter arises by a series of buds from the ento-

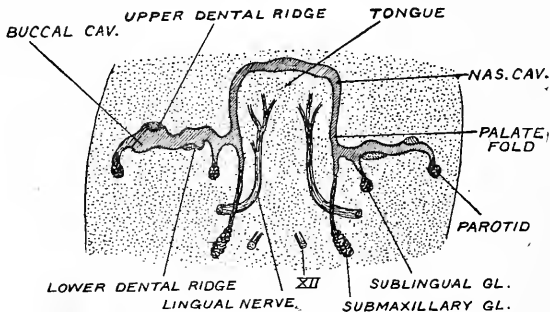


FIG. 265.—Showing the Origin of the Submaxillary and Sublingual Glands from furrows between the gum and tongue during the 7th week. The tongue projects between the maxillary folds into the nasal cavity. (After His.)

dermal lining of the groove, the former—the submaxillary—is developed by the depth of the entodermal furrow being enclosed in the mesoderm in the shape of a cord, which later becomes canaliculized and opens as a duct at the sublingual papilla, while the gland itself arises by a process of budding from the distal end of the enclosed entodermal cord. The sub-

¹ Prof. Wood Jones, *Journ. Anat.* 1918, vol. 52, p. 345.

² J. Schaffer, *Anat. Hefte*, 1907, vol. 33, p. 455 (Evolution of Epiglottis).

³ See reference under Paulet, p. 235; also W. Rubashkin, *Anat. Hefte*, 1912, vol. 46, p. 343.

maxillary ganglion is made up of nerve cells carried out from the geniculate ganglion during the outgrowth of the chorda tympani. The **parotid gland**, which is the first of the salivary glands to be developed (6th week), springs as a bud of entoderm from the lateral or bucco-alveolar recess of the primitive mouth (Fig. 265). Its duct is formed first as a groove, which later becomes enclosed to form a canal. It grows backwards in the connective tissue over the masseter, and at birth is comparatively superficial in position, but as the mandible and external auditory process grow, it sinks inwards to surround the styloid process, pushing the deep cervical fascia beneath it. In this way the stylo-mandibular ligament is formed from the fascia pushed in front of it. Its nerves are derived from the 3rd division

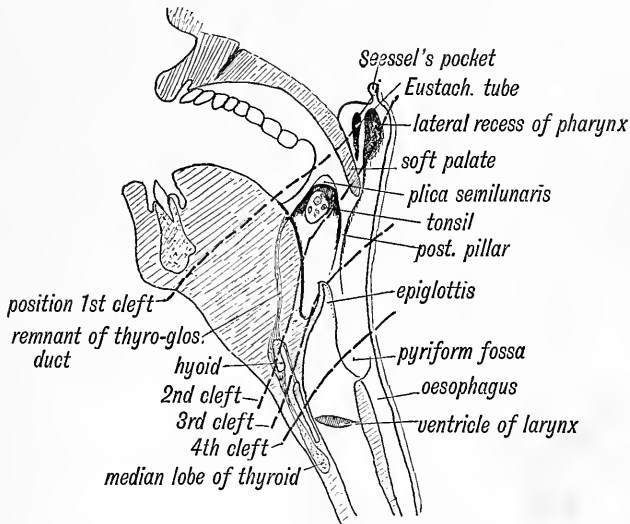


FIG. 266.—Showing the position of the Visceral Clefts in the Adult. The lines only indicate the approximate positions of the clefts. For instance, the soft palate is made up largely from the 3rd arch. See also Fig. 272.

of the fifth (auriculo-temporal). Salivary glands are accessory to the function of mastication, and hence are developed only in mammals.

Median Pharyngeal Recess.—In the middle line of the roof of the pharynx, just under the basi-occipital, there is a depression or recess of mucous membrane which receives this name. In Fig. 266 it is erroneously named *Seessel's pocket* which, as has been mentioned on page 107, disappears in the human embryo during the development of the pituitary gland. Its embryological significance is doubtful, but the site of its appearance corresponds to the point at which the notochord remained unseparated from the dorsal wall of the embryonic pharynx (Fig. 131). Lymphoid tissue is developed in its walls immediately after birth, and in the mucous membrane round it. It is developed behind the oral plate. The adenoid tissue of the naso-pharynx continues to increase in amount until the age of puberty, when it begins to undergo a slow process of atrophy (Symington).

The Tonsil.¹—The tonsil arises early in the 3rd month of foetal life from that part of the second cleft recess which is left between the soft palate and the tongue (Fig. 270, *B*). In the 4th month eight or ten isolated buds of entoderm push out from an elevation or tubercle situated in this recess or pocket, and grow into the mesodermal tissue in the wall of the pharynx (Fig. 268). The buds afterwards canalicularize and form the crypts and glandular tissue of the tonsil. Follicles of lymphoid tissue—for the tonsil must be regarded as a lymphoid structure—begin to collect round these glandular buds in the 5th month of foetal life.

Concerning the origin of the lymphoid cells, both of the tonsil and the thymus, there are two quite distinct theories. The more recent (Gulland's) is that the epithelial entodermal cells, which form the glandular buds of the tonsil, give rise to broods of lymphoid cells; the older and the better founded, that these lymphoid cells arise from the blood or surrounding connective tissue, creep in and form follicles round the glandular entodermal buds.

A fold of mucous membrane, the **plica triangularis** (Fig. 267), passes from the lower part of the tonsil to the anterior pillar of the fauces. It

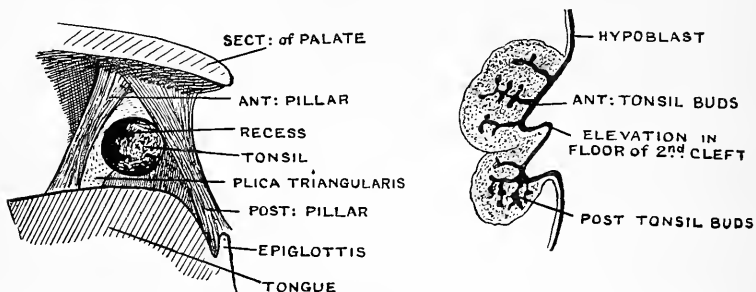


FIG. 267. The Tonsil in a Human Foetus of 8 months. (Hett and Butterfield.)

FIG. 268.—Section across the 2nd cleft recess showing the Outgrowth of the Tonsillar Buds. The elevation between the anterior and posterior groups forms the lower part of the plica triangularis. (After Hammar.)

represents the anterior part of the elevation or tubercle in which the glandular buds develop. Although present in the foetus, it commonly disappears in the adult. Its attachment to the tonsil marks a line of separation between an anterior and posterior group of tonsillar outgrowths (Fig. 268). The recess above the tonsil, sometimes crossed by a fold—the plica semilunaris—is a remnant of the recess of the second cleft in which the tonsil is developed (Fig. 267). In many mammals the tonsillar recess assumes the form of a funnel-like process resembling the finger of a glove, the blind end reaching almost to the angle of the jaw.

The tonsil is part of a great lymphoid system stationed along the alimentary canal. It reaches its fullest growth in youth, as is the case with the lymphoid system generally; when active growth of the system is over, and especially in the years of decay, it becomes markedly reduced in size. The upper part of the 2nd cleft recess is included with the 1st in the

¹ For an account of the comparative anatomy and development of the tonsil see paper by Secombe Hett and Butterfield, *Journ. Anat. and Physiol.* 1910, vol. 44, p. 35.

Eustachian tube (Frazer). The lower part of the 2nd recess, containing the tonsil, is separated from the Eustachian part by the growth forwards of tissue of the 3rd arch to help in the formation of the palatal folds in the latter part of the second month. Occasionally the tonsillar recess projects outwards, and comes in contact with a tubular fistula representing the cervical sinus (see Fig. 253).

The Pharyngeal Recess and Pharyngeal Tonsil.—At each side, the roof of the pharynx is produced outwards, behind the Eustachian tube and levator muscles of the palate, to form the **lateral recesses** of the pharynx (Fig. 266). In the recess, and especially on the posterior wall of the pharynx between the recesses and also in and round the median pocket, there is developed a submucous carpet of lymphoid tissue, the **pharyngeal tonsil**, which often becomes hypertrophied to form *adenoids* in youth.

The Lingual Tonsil.—That part of the tongue (pharyngeal) produced between the 2nd and 3rd arches is studded with mucous glands which are surrounded by nodules of lymphoid tissue—the collective glandular mass receiving the name of lingual tonsil. It will thus be seen that from the 2nd cleft and its neighbourhood is produced a circum-pharyngeal ring of lymphoid tissue of great physiological and pathological importance.

The Thymus.¹—The thymus arises in the same manner as the tonsil, only from the 3rd instead of the 2nd cleft (Fig. 270). The 3rd cleft is

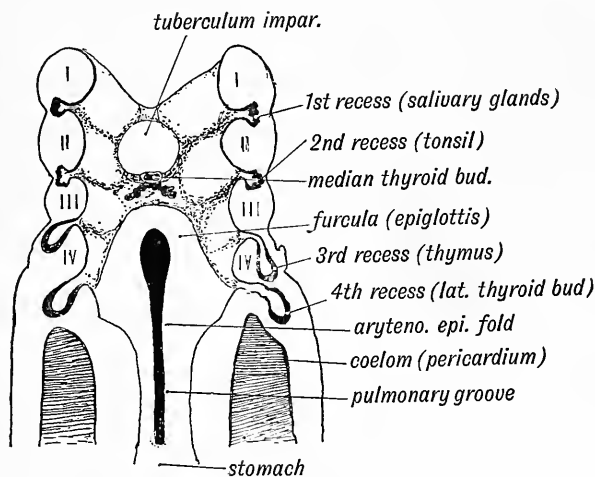
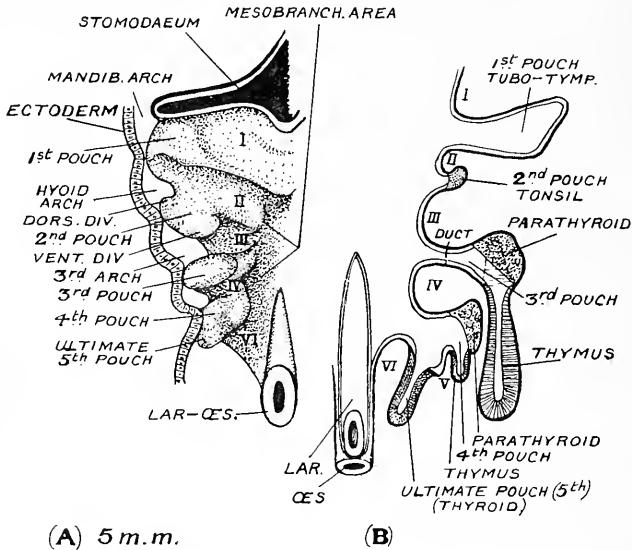


FIG. 269.—Showing the origin of the Tonsil, Thymus and Thyroid from the Internal Cleft Recesses during the 5th week. (After His.)

represented in the adult by the space in front, and on each side, of the epiglottis. It is crossed by the posterior pillars of the fauces, which represent a continuation of the palatal processes (Fig. 266). In the 6th

¹ T. H. Bryce, *Journ. Anat. and Physiol.* 1906, vol. 40, p. 91 ; P. Stoehr, *Anat. Hefte*, 1906, vol. 31, p. 409 ; J. A. Hammar, *Ergebnisse der Anat.* 1909, vol. 19, p. 1 ; *Anat. Hefte*, 1911, vol. 43, p. 201 (Thymus) ; Fraser and Hill, *Phil. Trans.* 1916, vol. 207 (B) p. 1 ; B. F. Kingsbury, *Amer. Journ. Anat.* 1915, vol. 18, p. 329.

week the 3rd pharyngeal pocket has assumed the form shown diagrammatically in Fig. 270, *B*, where its lower and hinder wall is represented as extended in the form of a flask-like process, lined by thickened entoderm, the embryological basis of the thymus. On the dorsal part of the same pocket there is another thickening representing the lower **parathyroid** or epithelial body, while the original mouth of the pocket has been drawn out to form a tubular process or duct. In Fig. 270, *A*, is represented another view of the 3rd pocket, during the 5th week of development. By the 7th week the ectodermal covering, shown in Fig. 270, *A*, has been invaginated to form the cervical sinus and vesicle, the latter being continuous with the thymic outgrowth. The neck of the glandular thymic



(A) 5 m. m.

(B)

FIG. 270, *A*.—The Lining Membrane of the Pharynx of a Human Embryo, 5 mm. long (5 weeks old), seen on its ventral aspect and showing the external configuration and relationships of the pharyngeal pockets. (After Grosser.)

FIG. 270, *B*.—A schematic representation of the pharyngeal pockets and the glandular structures rising from them in the 6th week of development. (After Grosser.)

pocket becomes separated from the pharynx in the 7th week and usually disappears, but a strand of tissue frequently persists and represents the stalk of the outgrowth (Fig. 271). By a species of secondary budding the thymic entodermal outgrowth becomes broken up into islands or separated acini. The epithelial acini proliferate and give rise to a meshwork of united cells (syncytium), in which broods of lymphoid cells appear during the 3rd month. The lymphoid cells—lymphocytes—become aggregated into follicles, where the production of lymphocytes is continued. All trace of the original epithelial cells disappears. The concentric bodies, known as the corpuscles of Hassall,¹ were at one time supposed to represent remnants of

¹ Dr. E. T. Bell defends the theory of their Epithelial origin, *Amer. Journ. of Anat.* 1906, vol. 5, p. 30.

the epithelium, but they are now known to be produced from single cells, which divide without a separation of the daughter cells thus formed. Hassall's corpuscles also arise from capillaries, some of which, after invading the thymus, become broken up into segments. The endothelial cells lining those segments may proliferate, occlude the lumen, and thus give rise to a Hassall's corpuscle (Nussbaum) (see also p. 335). The surrounding mesoderm supplies the connective tissue stroma and capsule of the thymus. The lateral lobes come together under the ventral aortae and pericardium during the 7th week, and ultimately assume a thoracic position along with these structures. The pointed upper extremity of each lateral lobe can be traced upwards in the fully developed foetus, under the lateral lobes of the thyroid towards the thyro-hyoid membrane (Figs. 171, 253). These apical strands represent the stalk of the thymic buds. Thymus

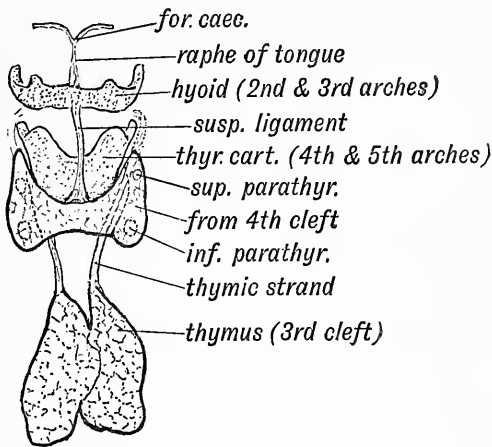


FIG. 271.—Diagram of the Thyroid and Thymus. The position of the parathyroids on the posterior aspect of the lateral lobes of the thyroid is indicated.

buds also arise from the 4th pouch (Fig. 270), and from the cervical sinus, but these never proceed beyond a rudimentary stage in the human embryo.

While Beard regards the thymus as the parent source of all the white blood corpuscles of the body, many interpret the appearances in quite an opposite manner and are of opinion that the leucocytes are brought within the epithelial element of the thymus along with the mesodermal invasion. Professor Bryce has demonstrated that, white blood corpuscles appear in vertebrate embryos before any are seen in the thymus.

The thymus reaches its fullest growth in early childhood (3rd or 4th year), and continues large as long as the body is in a state of active growth. It begins to shrivel up when maturity is reached, and only a remnant is left as a rule, less remaining in men than in women. It receives its blood supply from the 4th aortic arches through the internal mammary. In manner of origin it resembles the tonsil; indeed it may be regarded as a buried tonsil. There is a profuse production of lymphoid cells in the gill clefts of fishes, many of which wander out, and by their phagocytic properties help to keep the gill surfaces clean. This fact throws some light on

the origin of so much lymphoid tissue from the second and third cleft recesses in higher animals.

The Thyroid.¹—The site at which the thyroid gland arises is shown in Fig. 269—on the floor of the pharynx behind the mandibular arch and exactly in the middle line. The entoderm of the retro-mandibular furrows gives rise to a saccular diverticulum almost as soon as the fore-gut becomes differentiated—early in the 4th week of development. Immediately in front of the thyroid evagination arises the buccal part of the tongue; behind it the pharyngeal part, the foramen caecum in the sulcus terminalis remaining to mark the site of origin. The entodermal vesicle thus formed grows downwards and backwards through the tissue in which the body of the hyoid will be formed and as it extends, bifurcates. The stalk of the evagination, at first hollow and representing a duct, quickly becomes solid, breaks up, and by the 6th week has disappeared. The epithelium of the evagination proliferates, and in the 7th week forms a transverse plate ventral to the larynx (Fig. 252). The plate is invaded and broken up into reticulating columns by the surrounding mesoderm. In the 3rd month the epithelial cells become arranged as follicles; these at a later date are converted into vesicles. The original plate assumes a bent or horse-shoe form, the middle part forming the isthmus, the side parts the lateral lobes (Fig. 271).

The thyroid is present in all vertebrates and, although it arises in a manner which suggests that at one time it was a gland of the mouth, yet in no animal does the duct persist. Its early origin in the embryo and its universal distribution in vertebrates point to the antiquity and importance of its function. We now know that duct glands have a double function, producing both external and internal secretions. It is reasonable to suppose that, as regards the thyroid, its excretory function has been lost.

Thyro-glossal Duct.—In the great majority of subjects the thyro-glossal duct or stalk completely disappears at the commencement of the 2nd month of development; the foramen caecum marks one extremity, while a ligament or a **pyramid** of thyroid tissue prolonging the isthmus towards the hyoid bone often marks the other extremity (Fig. 271). The pyramid of the isthmus may carry on it a detached part of the thyro-hyoid muscle—the **levator glandulae thyroideae**. The body of the hyoid bone is developed in the tract of the thyro-glossal duct (Figs. 271, 272) and splits it up. Remnants of the duct or of secondary detached acini of the thyroid may persist and form cysts or thyroid tumours in the base of the tongue above the hyoid, and commonly between the genio-glossus muscles. They may also occur between the hyoid and thyro-hyoid membrane. The supra-hyoid or infra-hyoid bursae may also become cystic, and may be mistaken for thyro-glossal cysts (see Fig. 272).

In lower vertebrates the lateral lobes of the thyroid are stationed under the mandible. It is not uncommon to find in the right submaxillary region of man a thyroid tumour or cyst, evidently arising from an arrest in the descent of a part or of the whole of a lateral lobe. Aberrant masses

¹ Edgar H. Norris, *Amer. Journ. Anat.* 1916, vol. 20, p. 411; 1918, vol. 24, p. 443.

of thyroid are often met with in the neck, and frequently become the site of cystic tumours. Occasionally the lumen may persist in the median thyroid and open as a fistula in front of the larynx (Fig. 272).

Ultimate Branchial Bodies.—In Fig. 270, *B*, is represented the entodermal outgrowth from the 5th or ultimate pharyngeal pouch. At one time it was supposed that the entodermal outgrowth—the ultimate branchial body—gave rise to the greater part of the lateral lobes of the thyroid. They do give rise to tissue which is thyroïdal in structure, often containing tube-shaped vesicles. The tissue so produced is applied to the dorsal aspect of the lateral lobes of the thyroid, but forms a very small part of their glandular mass. Like the thymic buds they lose their connection with the embryonic pharynx by the 7th week. The pyriform fossa, within the ala of the thyroid cartilage marks their point of origin (Fig. 272). The

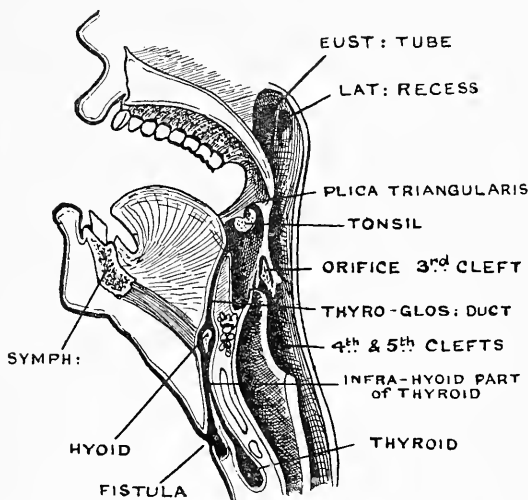


Fig. 272.—Section of the Pharynx to show the Track of the Median Thyroid Outgrowth. In rare cases there is a fistula connected with the thyroid, which opens in front of the larynx. The point of origin of the thymus outgrowth from the 3rd cleft may be marked by a recess containing lymphoid tissue as is represented in the figure. The pyriform fossa occurs at the site of the 4th and 5th clefts. The group of mucous glands in front of the epiglottis may give rise to cystic tumours.

blood supply suggests a double origin for the thyroid gland, for while the superior arteries supply the area formerly assigned to the median outgrowth, the dorsal parts of the lateral lobes are nourished by the inferior thyroid branches of the 4th aortic arch.

Para-thyroids.¹—There are usually two para-thyroid or **epithelial** bodies on each side, an upper and a lower (Fig. 271). Both are usually applied

¹ For a full account of the comparative anatomy of the para-thyroids see Dr. Forsyth's Memoir in *Journ. Anat. and Physiol.* 1908, vol. 42, pp. 141, 302. He found that the para-thyroids are irregular in number and often aberrant in position, and that it is very difficult to distinguish microscopically between embryonic thyroid tissue and adult para-thyroid tissue. The para-thyroids were discovered by Sandstrom in 1880. See also F. D. Thompson, *Phil. Trans.* 1911, vol. 201, Ser. B, p. 91.

to the deep or posterior aspect of the thyroid body, the upper being situated amongst the terminal branches of the superior thyroid artery, the lower amongst the branches of the inferior. They are flattened bodies, about 6 to 8 mm. in diameter, yellowish in colour when contrasted with the substance of the thyroid, but they cannot be recognized with certainty except by their microscopical structure. Their origin is shown in Fig. 270; the lower bodies arise from the dorsal recess of the 3rd pair of pouches; they are drawn into a low position by their attachment to the stalk of the thymus (see Fig. 270). The upper para-thyroids arise from the 4th pair of pouches (Fig. 270), and become more or less united to the ultimate branchial bodies, and with these are applied to the dorsal aspect of the lateral masses of the thyroid. In structure they are made up of reticulating columns of cells, with vessels arranged between the columns, thus resembling in structure the carotid body, and probably also in nature and origin the medullary part of the supra-renal. Their presence is essential to the function of the thyroid body.

Carotid Bodies.—The carotid body lies at the inner side of the fork between the internal and external carotid arteries. The commencement of the internal carotid represents the artery of the 3rd arch; that of the external carotid, the ventral aortic trunk. The body is developed near the 3rd pharyngeal pouch with the thymus (Fig. 253). In the carotid fork nerve cells assemble which are derived from the superior cervical ganglion; the body is linked to the superior cervical ganglion by numerous nerve fibrils. It is essentially parasympathetic in nature, being made up of chromaffin cells, similar to those of the medulla of the adrenal bodies.

CHAPTER XIX.

ORGANS OF DIGESTION.

Divisions of the Alimentary Tract.¹—It is always advantageous to approach the development of every system of the body by a recapitulation of the various evolutionary stages, so far as these stages are known to us. As regards the evolution of the various parts of the alimentary system, comparative anatomy does not help us greatly, because in even the lowest forms of vertebrates the main parts are already present—the mouth,

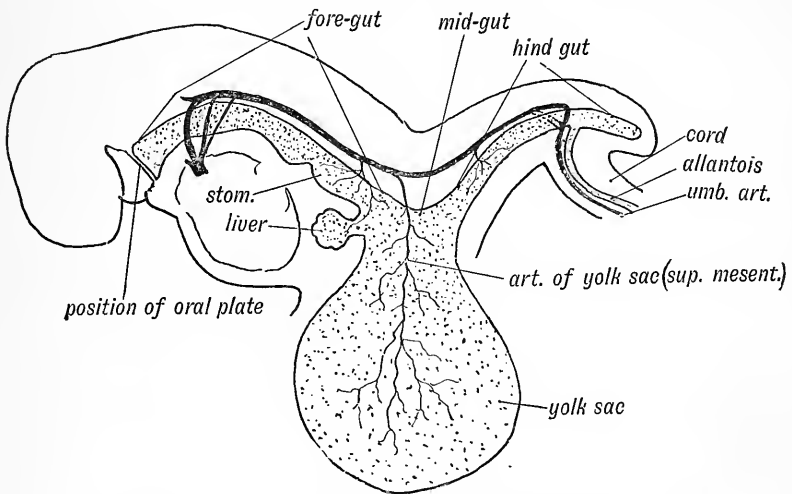


FIG. 273.—The Form of the Alimentary Canal in a Human Embryo of the 4th week.

oesophagus, stomach, liver and intestine. In tracing the development of the earliest digestive cavity (archenteron) of the human embryo (p. 38) we saw that its origin was similar to that of the lower invertebrates and that its first mouth apparently became converted into the blastopore, primitive streak and cloacal membrane. A new mouth is formed by the breaking down of the bucco-pharyngeal membrane (oral membrane, Fig. 273) early in the third week; we shall see that a new kind of vent or anus is formed at

¹ For literature on development of alimentary system see A. Oppel, *Ergebnisse der Anat.* 1905, vol. 15, p. 207; 1906, vol. 16, p. 216; O. Grosser, *Verhand. Anat. Gesellsch.* 1911, p. 173; Keibel and Mall's *Manual of Human Embryology*, 1912, vol. 2, p. 291.

a later stage in the development of the human embryo—namely, at the end of the 2nd month of development. There are other reasons why comparative anatomy does not help us to understand the early stages in the development of the alimentary system. They will be understood by a reference to Fig. 273. In the human embryo a large part of the alimentary cavity has been specialized and precociously developed to form the yolk sac for the nourishment of the embryonic tissues; the embryonic adaptations mask and obliterate the ancestral stages (see page 35).

With the development of the cephalic and caudal evaginations of the embryonic plate the archenteron becomes differentiated into three parts (Fig. 274)—the **Mid-gut**, which represents the body and chief part of the primitive cavity; the **Fore-gut** and **Hind-gut**. There can be no doubt these represent three functional divisions. The mid-gut is supplied by the superior mesenteric artery and serves for one kind of digestion and absorption; the hind-gut, supplied by the inferior mesenteric artery, is mainly excretory in nature; the fore-gut, separated by the outgrowth of the liver from the mid-gut, is supplied mainly by the coeliac axis and serves the preparatory purposes of digestion. The pharynx, respiratory tract, oesophagus, stomach, liver and pancreas represent parts of the fore-gut. The hind-gut gives rise to the colon from the splenic flexure to the anus; the allantois, bladder and urethra are also separated from its hinder end—the cloaca.

Differentiation of Parts.—How rapidly the various parts of the alimentary system are differentiated during the 4th week of development will be seen by comparing Figs. 274 and 275. Fig. 274, which represents the alimentary tract of a human embryo near the beginning of the 4th week, shows the pharynx large, the lung bud beginning to evaginate from the floor of the fore-gut just behind the pharynx and at this date lying directly under the occipital part of the head; the oesophagus and stomach and first part of the duodenum scarcely marked off from one another, all of them lying on the dorsal wall of the pericardium and lying under the cervical segments of the embryo. The evagination to form the liver indicates the junction of the fore-gut with the mid-gut. The latter division is in wide communication with the yolk sac. The various parts of the hind-gut are already indicated. The condition towards the end of the 4th week is shown in Fig. 275. The oral membrane is gone; the pharynx is relatively smaller; the outgrowth of the pulmonary system is now very apparent, the oesophagus and stomach are longer and narrower; the liver outgrowth has become massive; the mid-gut is tubular, and the neck of the yolk sac reduced to a duct (vitello-intestinal duct). The parts of the hind-gut have assumed a more definite shape.

Primitive Mesentery and Coelom.¹—It will be remembered that almost as soon as it appears, the mesoderm is cleft into two layers—an outer applied to the ectoderm to form the somatopleure or body wall, and an inner to the entoderm or archenteron to form the visceral wall or splanchnopleure. The cavity formed by the cleavage of the mesoderm is the coelom (Fig. 39). Originally the cavity was designed for the purposes of excretion; its wall

¹ Broman, *Ergebnisse der Anat.* 1905, vol. 15, p. 332.

also served as the nidus for the reproductive cells. In vertebrates the coelom came to serve the purposes of a large bursa, in order that the muscular movements of the digestive canal, lungs and heart might proceed without undue friction. Hence the alimentary canal is developed within the cavity of the coelom, being situated within the median partition, which separates the right coelomic space from the left. The median partition suspends the alimentary canal to the dorsal or vertebral wall of the body cavity, and forms the **primitive dorsal mesentery**; the part of the median partition which fixes the tract to anterior or ventral wall of the body cavity

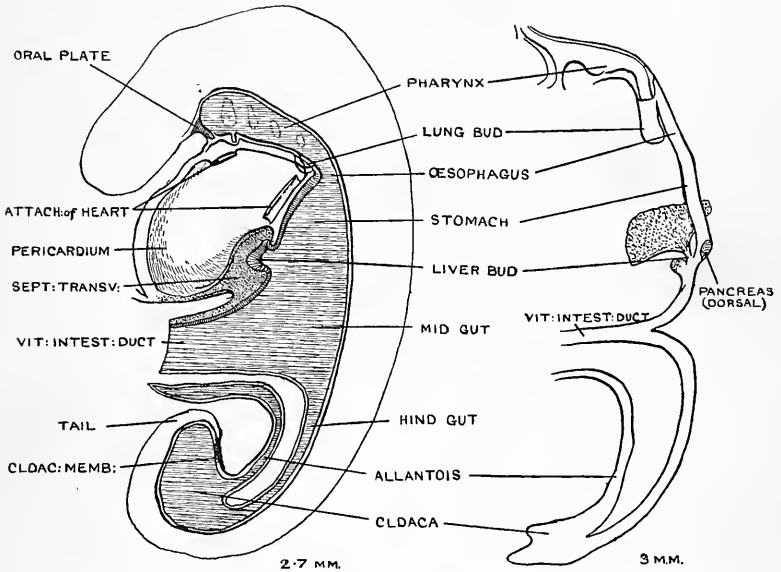


FIG. 274.—The Alimentary System of a Human Embryo 2.5 mm. long, and near the commencement of the 4th week of development. (Professor Peter Thompson.)

FIG. 275.—The Alimentary System of a Human Embryo, although only 3 mm. long, is in the stage of development reached at the end of the 4th week. (After Professor Broman.)

forms the **primitive ventral mesentery** which, however, is formed only in connection with the fore-gut and the cloacal segment of the hind-gut, all the rest being destitute of a ventral mesentery from the beginning. Hence the right and left coelomic spaces in the abdomen are thrown into one, and form the peritoneal cavity. The only parts of the alimentary canal which never come to lie within the coelom are the anterior part or pharynx and the most posterior part of the cloaca. The anterior part of the coelomic space forms the cavity of the pericardium, which lies beneath the pharynx (Fig. 274); it is separated from the peritoneal space by a transverse partition—the **septum transversum**,¹ already well marked at the beginning of the 4th week. The primitive oesophagus crosses the upper or dorsal border of the septum transversum (Fig. 279). At each side of it is situated a

¹ P. Thompson, *Journ. Anat. and Physiol.* 1908, vol. 42, p. 170.

communication between the pericardial and peritoneal spaces—the **pleuro-peritoneal passages**. These two passages are separated not only by the primitive oesophagus, but also by the primitive median mesentery, which encloses the oesophagus (Fig. 279).

Oesophagus.—In the 4th week the oesophagus of the human embryo resembles that of a fish; it is merely a sphincter or constricted part between the pharynx and stomach (Fig. 274). During the 6th and 7th weeks, when the neck is being differentiated, and the pharynx and head separated from the heart and thorax, the oesophagus undergoes a rapid

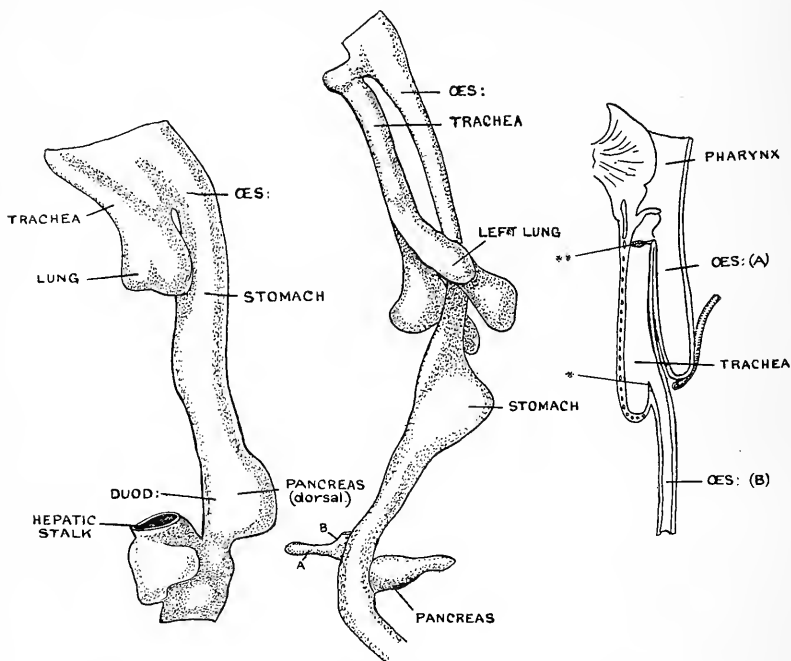


FIG. 276.—Fore-gut of an Embryo in the 4th week of development. (Broman.)

FIG. 277.—Fore-gut of an Embryo at the end of the 5th week of development. *A*, hepatic stalk; *B*, ventral pancreatic bud. (Broman.)

FIG. 278.—Irregular Separation of the Trachea and Oesophagus. The upper or pharyngeal part of the oesophagus forms a blind sac; the lower part passes from the trachea to the stomach. The normal trachea—oesophageal septum—is marked *; the abnormal septum **.

elongation. The chief cause of the elongation of the oesophagus is to be sought for in the development of the lungs and pleural cavities (Fig. 277), by which the stomach is forced backwards in the body cavity. The oesophagus is of double origin; the upper or paratracheal part is derived with the trachea from the retropharyngeal segment of the fore-gut; the lower or retrotracheal part arises from the pregastric segment of the fore-gut. In the 5th week the pulmonary bud and tracheal groove are being separated from the oesophagus, the lateral septa which effect the separation, beginning behind and spreading forwards (Figs. 276, 277). Children are sometimes born in which the process of separation has taken place in an irregular

manner (Fig. 278). The paratracheal part ends blindly, and is surrounded by striated pharyngeal musculature; the retrotracheal part opens from the trachea, and is covered by non-striated muscle.¹ The oesophagus is at first lined by columnar epithelium, but in the 2nd month, as it elongates the epithelium proliferates, forming several irregular layers, which almost occlude the lumen of the tube for a time. In the 5th month glands are formed in the submucous tissue. In the 6th week the oesophagus is only 2 mm. long; at birth it measures 100 mm. (4 inches). Its commencement is surrounded by a sphincter formed by part of the inferior constrictor of the pharynx; above this sphincter, in later life, a pouch (**retropharyngeal diverticulum**) may arise; such pouches are never congenital in origin.

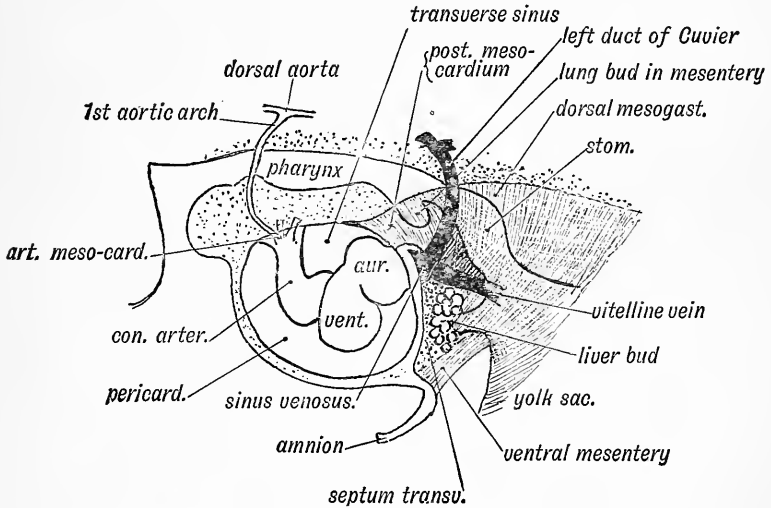


FIG. 279.—The Mesentery of the Fore-gut and its Contents, viewed from the left side (schematic).

At the lower end the oesophagus is also closed by a sphincter. The muscle coats are differentiated in the 7th week, the circular first, the longitudinal later.

Development of the Liver.²—Before proceeding to describe the development of the stomach, it is convenient to deal first with the liver, because the manner in which this viscus arises gives the key to the complicated developmental changes of the abdominal viscera. The human liver in its development repeats broadly the forms met with in ascending the animal scale. In amphioxus the liver is merely a caecal diverticulum of the digestive canal; in amphibians it is a modified tubular

¹ See Keith, *Brit. Med. Journ.* 1910, vol. 1, p. 301. For development of mucous membrane see F. P. Johnson, *Amer. Journ. Anat.* 1910, vol. 10, p. 521.

² O. Charnock Bradley, *Journ. Anat. and Physiol.* 1909, vol. 43, p. 1; F. P. Mall, *Amer. Journ. Anat.* 1906, vol. 5, p. 227; F. T. Lewis, *Keibel and Mall's Manual of Human Embryology*, 1912, vol. 2, p. 403; Prof. F. Thompson, *Journ. Anat.* 1914, vol. 48, p. 222. See also references to Barniville (p. 47) and Waterston (p. 18); Prof. Frazer, *Journ. Anat.* 1919, vol. 54, p. 116.

gland—the hepatic cells being arranged in cylinders around the bile ducts. In mammals the tubular arrangement is lost and a lobular form substituted. In every case it is so placed that the blood, laden with the products of absorption from the alimentary tract or from the placenta, must come into intimate relationship with the hepatic tissue before passing into the general circulation of the body.

To understand the development of the liver, the condition of parts at the commencement of the 4th week must be studied. At this time, the anterior wall of the yolk sac and that part of the fore-gut which becomes the stomach, lie in the dorsal wall of the septum transversum (Fig. 274), or to be more accurate, in the substance of the dorsal and ventral mesentery

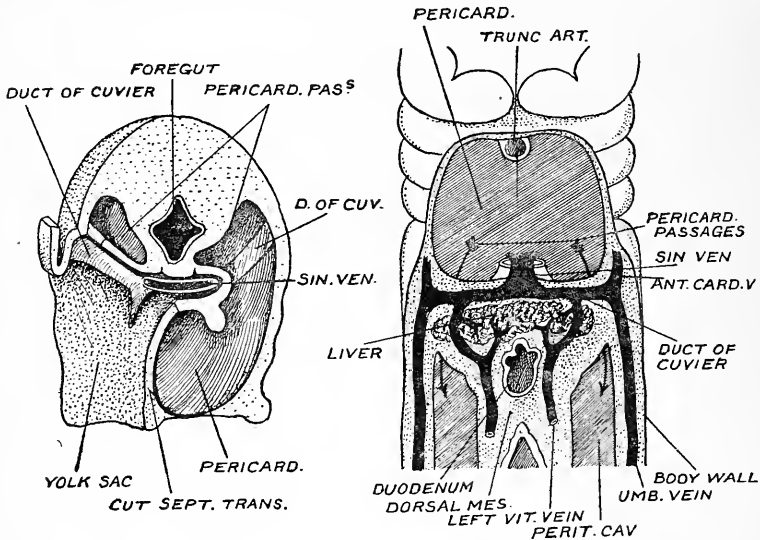


FIG. 280.—Dissection of the Septum Transversum of a Human Embryo early in the 4th week of development. The right half is cut away to expose the yolk sac. (After Low.)

FIG. 281.—Coronal Section of the Septum Transversum of a Human Embryo in the 5th week of development, showing the liver trabeculae invading the terminal parts of the vitelline veins. (After His.)

which have not yet been differentiated from the septum transversum (Fig. 279). Two other views of the septum transversum are given in Figs. 280, 281, which will assist the reader to understand the early relationship of the liver. When the liver bud grows out, it springs from the junction of the fore-gut and yolk sac (Fig. 279); and spreads into the tissue which becomes the ventral mesentery of the fore-gut. The part of the gut from which it arises afterwards becomes the second stage of the duodenum. The hepatic bud is at first a hollow, a fold-like diverticulum of the fore-gut, lined with entoderm; from the upper or cranial end of the diverticulum arises the outgrowth of liver tissue; its lower or caudal end becomes the gall bladder and main bile ducts (Fig. 276). The diverticulum is surrounded in the mesogastrium by a mass of mesodermal cells which

form the vessels, capsule and connective tissue of the liver. From the hollow hepatic diverticulum arise right and left solid processes of entodermal cells, which invade and form masses round the right and left veins from the yolk sac—the vitelline veins (Figs. 279, 281). Professor Bradley¹ has pointed out that the right and left masses do not correspond to the right and left lobes of the fully formed liver; the separation between the right and left lobes is formed late, and has no functional significance. A line from the fundus of the gall bladder to the caval impression divides the liver into embryonic and functional right and left halves (Cantlie).

The hepatic buds are developed just behind the sinus venosus and between both the vitelline and umbilical veins which are also situated in the ventral mesentery (Figs. 279, 281, 282). The veins are broken up by the ingrowth; from them starts an invasion of sinus-like capillaries which, with the surrounding mesoderm, penetrates the liver bud and breaks the solid entodermal processes into reticulating cylinders. According to F. T. Lewis the hepatic processes perforate and proliferate within the lumina of the vitelline veins, the venous capillaries thus arising directly from venous spaces. Secondary processes arise from the primary hepatic reticulating cylinders and form smaller and smaller meshes of hepatic cells. The hepatic cells, first grouped in trabeculae, become arranged in lobular units; round the periphery of the units are the terminal portal venules; in the centre of each unit is the beginning of a tributary of the hepatic vein; the portal or placental blood as it passes from the periphery to the centre of each lobule is exposed to the action of the liver cells. Growth takes place by successive division or dichotomy of the lobules, the chief areas of proliferation being always at the surface of the organ or subcapsular. Growth is particularly rapid during the 2nd and 3rd months, the liver reaching its largest relative size at this time. Up to the 10th week, when the foetus is 42 mm. long, the right and left halves have grown symmetrically, but then occurs the retraction of the bowel from the umbilical cord and the enlargement of the stomach, leading to an atrophy of part of the left lobe. The *ducts of the liver*, unlike those of any other gland, arise by a secondary process. Undifferentiated tissue lying along the distribution of the portal vein in the liver group themselves in cords, develop lumina, become covered by mesodermal tissue and thus form the intra-hepatic bile ducts.

Veins of the Liver.—Within the liver the two vitelline veins become divided so as to form two sets of vessels—afferent or distributing and efferent or collecting veins (Fig. 282). In the 5th week a number of remarkable changes occur: (1) The left umbilical vein, which opens at first in the left duct of Cuvier, establishes a communication with the portal sinus in the transverse fissure of the liver (Figs. 281, 282, 283); (2) the right umbilical vein disappears; (3) a new channel—the *ductus venosus*—is opened between the portal sinus and the inferior vena cava; (4) the right vitelline vein, all except its terminal part, becomes obliterated (Fig. 283).

¹ *Journ. Anat. and Physiol.* 1909, vol. 43, p. 1.

Gall Bladder and Bile Ducts.¹—The hepatic diverticulum, from which the liver buds arise, may be regarded as a direct extension of the wall of the fore-gut. From its hinder part (Fig. 276) are developed

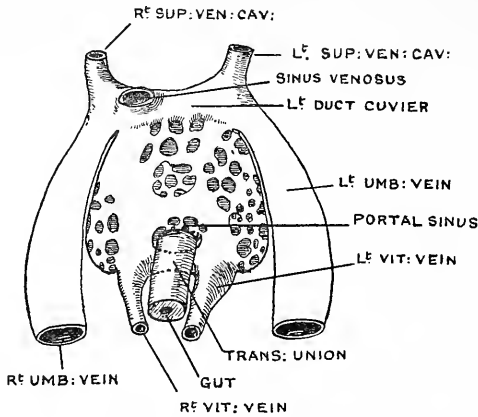


FIG. 282.—The Liver Mass invading the Vitelline Veins during the 4th week of development. (Professor Mall.)

the common bile duct, the gall bladder, and the cystic duct formed at the junction of the gall bladder and common bile duct. The hepatic ducts arise within the stalks of the solid hepatic buds. At first the gall bladder

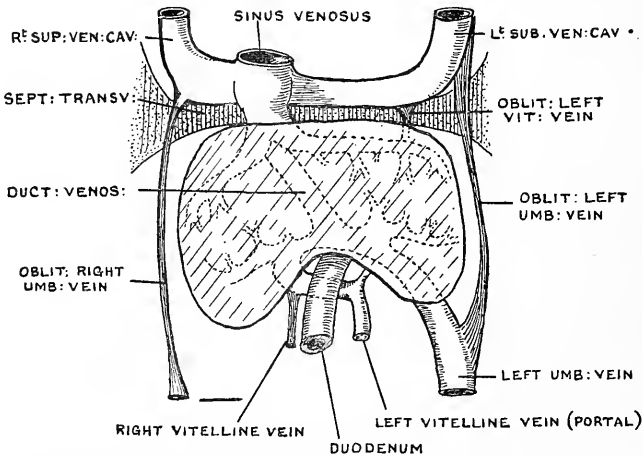


FIG. 283.—Diagram to show the Transformation in the Veins round the Liver at the end of the 5th week of development. (After Professor Mall.)

lies in the ventral mesentery (gastro-hepatic omentum)—a position which is permanent in some vertebrates and may occur as a rare anomaly in man. In the second month it becomes embedded in the hepatic tissue, its fundus appearing on the diaphragmatic surface; at a later date it

¹ A. Pensa, *Anat. Anz.* 1912, vol. 41, p. 155.

assumes its superficial position. The lumen of the ducts is occluded by an epithelial proliferation until the 3rd month; bile enters the gall bladder in the 6th month. Originally its veins end in the adjoining hepatic tissue. Occasionally the bud for the gall bladder divides, giving rise to a bifid or double gall bladder. Round the termination of the common bile duct a sphincter is developed from the musculature of the duodenum. The manner in which the common bile duct, hepatic artery and portal vein come to occupy the free edge of the ventral mesogastrium will be described in another paragraph.

Separation of the Liver from the Septum Transversum.—As the liver develops, the dorsal and ventral mesenteries of the fore-gut, in the

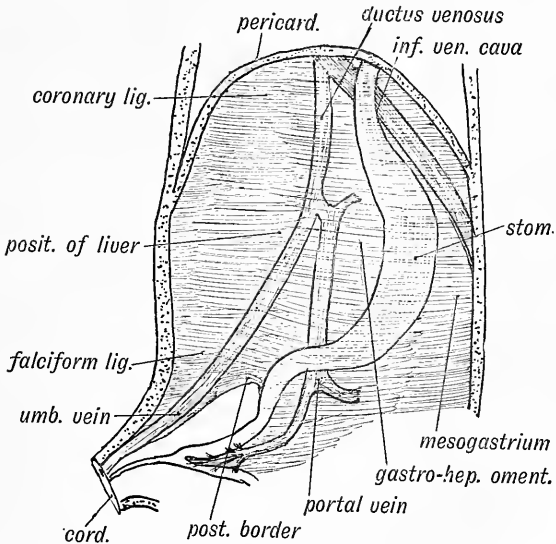


FIG. 284.—The origin of the Peritoneal Ligaments connected with the Liver. Diagram to show the foetal relationship of the ventral mesentery to veins and the stomach, the liver being removed.

substance of which the liver and stomach are formed, become differentiated from the tissues of the septum transversum. The typical arrangement of these membranes, as seen in reptiles, is shown in Fig. 284. In the dorsal mesentery (mesogastrium) lie the inferior vena cava and arteries of the fore-gut; in the ventral mesentery (gastro-hepatic omentum) are contained the terminal parts of three veins—the umbilical, portal and inferior vena cava, the last vessel reaching the ventral mesentery by passing to the right of the oesophagus. The liver develops within both ventral and dorsal mesenteries, but that part of the mesentery in which it and the inferior vena cava lie—the **mesohepar**—becomes separated from the part which is occupied by the bile ducts, portal vein and the stomach. Broman found that this separation, which occurs in all higher vertebrates, takes place towards the end of the 4th week in the human embryo, by the development of a recess in the mesentery—the **Mesenteric Recess**—which

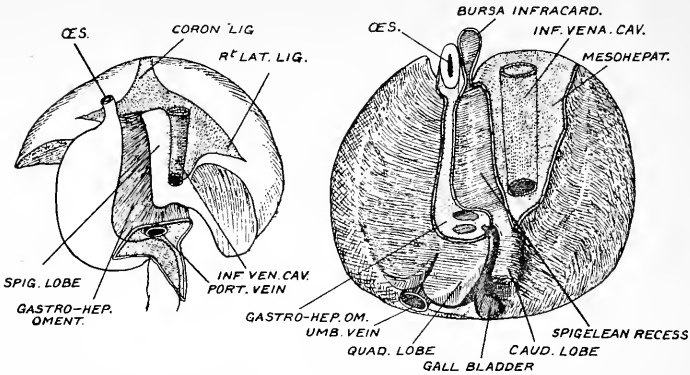


FIG. 285.—The Liver viewed from behind to show its relationship to the Gastro-hepatic Omentum, part of the Ventral Mesentery.

FIG. 286.—The Visceral Surface of the Liver of a Foetus, 16 mm., in the 7th week of development. (P. Thompson.)

commences to the right side of the duodenum, and extends forwards (see Fig. 287). The **mesenteric recess**¹ (bursa omentalis, Broman) forms the vestibular or hepatic part of the lesser sac of the peritoneum, and extends

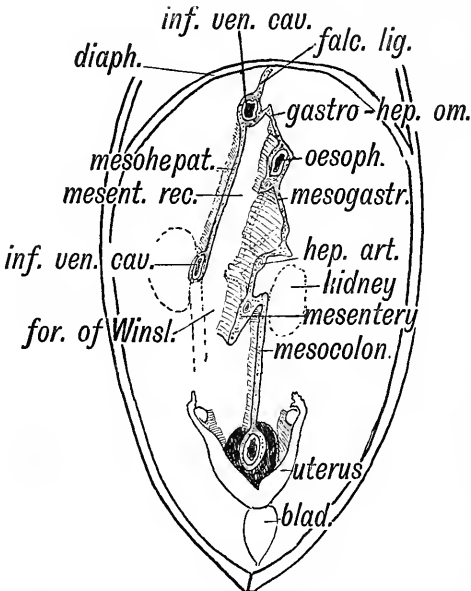


FIG. 287.—Diagram of the Primitive Attachments of the Visceral Mesenteries to the Posterior Wall of the Abdomen as seen in a Low Primate (Lenur Coronatus). The condition illustrates the earlier developmental phases of the human foetus.

from the foramen of Winslow to behind the Spigelian lobe of the liver (see Figs. 287, 288 and 286). When the liver and stomach are removed

¹ See F. T. Lewis, *Anat. Rec.* 1916, vol. 10, p. 220.

in the course of dissection, the attachment of the mesohepar will be seen to bound the Spigelian part of the lesser sac on the right, while on its left side, the dorsal mesogastrium has been evaginated to form the main body of the lesser sac (Fig. 288). Thus it will be seen that the dorsal and ventral mesenteries of the fore-gut are split into a right lamina—the mesohepar, and a left lamina—the mesogastrium—by the development of a recess which forms the earliest and first part of the lesser sac. The mesenteric recess at first extends forwards in the mesentery of the oesophagus almost to the right lung bud—a condition which is constant in reptiles. When the lungs expand and the diaphragm is being formed during the 7th week,

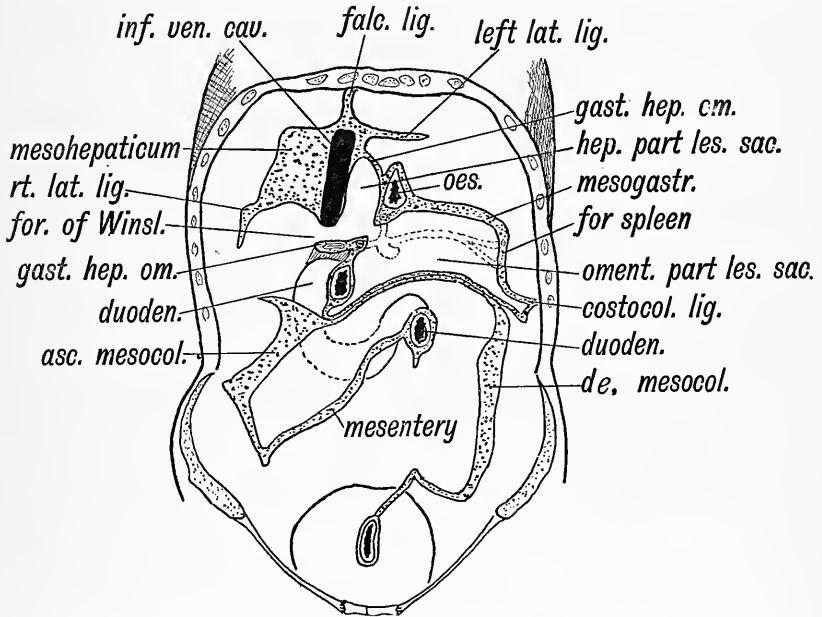


FIG. 288.—Diagram of the Attachments of the Visceral Mesenteries to the Posterior Abdominal Wall of an Adult. The three chief modifications seen, when compared with Fig. 246, are (1) the extensive adhesion of the mesogastrium, (2) of the mesocolon, and (3) mesentery of small intestine, to the posterior wall of the abdomen.

the apical part of the mesenteric recess is cut off and left within the thorax—to the right of the oesophagus, and just above the diaphragm. To this detached part, Broman has given the name of **infra-cardiac bursa** (Fig. 286). It usually disappears at the end of foetal life, but a remnant can often be found in adults if careful search is made.

The Ligaments of the Liver.—When the liver separates from the septum transversum towards the end of the 2nd month of development, it is attached to the walls of the abdomen by peritoneal ligaments derived from the dorsal and ventral mesenteries of the fore-gut (Figs. 284, 285). These are the following:

1. **The gastro-hepatic omentum** is that part of the ventral mesentery which passes from (1) the oesophagus, (2) lesser curvature or ventral

border of stomach, and (3) first stage of duodenum to (1) the diaphragm, (2) the posterior part of the longitudinal fissure of the liver, the ductus venosus lying within its hepatic attachment, and (3) the transverse fissure of the liver (Fig. 285). The portal and umbilical veins lie in the ventral mesentery (Fig. 284); the hepatic artery passes by it to the liver. The right or free border of the gastro-hepatic omentum, with the falciform ligament containing the remnant of the umbilical vein, represents the posterior border of the primitive ventral mesentery (Fig. 284).

2. **The falciform ligament**, containing the umbilical vein, also represents part of the ventral mesentery (Fig. 284). At an early stage the umbilical veins reached the sinus venosus by passing through the septum transversum. The terminal parts of both veins become obliterated (Fig. 283); the new terminal channel for the left vein is formed in the ventral mesentery.

3. **The coronary, the right and left lateral ligaments, and the attachments to the vena cava and diaphragm.**—These ligaments, which are the chief

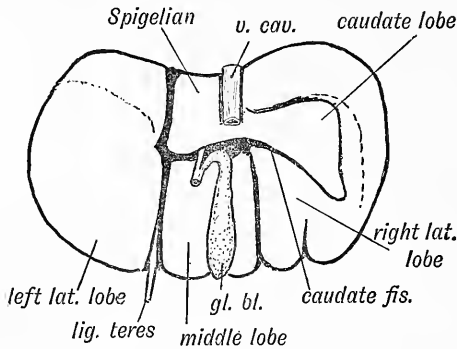


FIG. 289.—Diagram of a Mammalian Liver viewed from behind and below.

hepatic bonds, are derived from the mesohepar in the later part of the 2nd month, when the liver is being separated from the diaphragm by invading pockets or recesses of peritoneum. It would be extremely convenient to retain the term mesohepar to designate the bonds between the liver and diaphragm in the adult, looking on the right and left lateral ligaments as merely processes of the mesohepar.

Morphology of the Liver.¹—The liver of orthograde (upright) animals (man, anthropoids) differs widely in form and lobulation from that of mammals generally, but Professor Arthur Thomson has shown that traces of the fissures and lobes of the typical mammalian liver can be seen in the human organ. The liver of a dog or dog-like ape consists of three main lobes—right, middle and left—and two accessory lobes—the caudate and Spigelian (Fig. 289). In man the right and middle lobes have fused, but traces of the fissure which separates them (the right lateral fissure) are

¹ I have dealt with some of the factors which determine the shape of the liver in lectures on enteroptosis; see *Lancet*, 1903, March 7th and 14th. For cases of malformation of liver see E. Barclay-Smith, *Journ. Anat. and Physiol.* 1909, vol. 43, p. 346; Prof. P. Thompson, *Journ. Anat.* 1914, vol. 48, p. 222.

frequently to be seen in the liver of the newly born child (Fig. 290). The **caudate lobe** has been reduced in man to a vestige, but in the third month foetus it is of considerable size (Figs. 286, 290). It projects from the liver at the upper boundary of the foramen of Winslow; in many animals it rivals the right lobe in size. The caudate fissure separates the caudate from the right lobe, and a trace of this fissure is very frequently to be seen in the human liver (Fig. 286). Irregular lobulation of the liver is not uncommon; the condition seen in the 6th week, when the gall bladder and umbilical vein occupy a common fissure, may be retained. The quadrate lobe arises in the 7th week (Fig. 286) from the left lobe and grows across the fissure occupied by the umbilical vein to occupy the space between the vein and gall bladder (P. Thompson).

Changes in the Liver after Birth.—During foetal life the liver increases rapidly in size in comparison with the other abdominal organs.

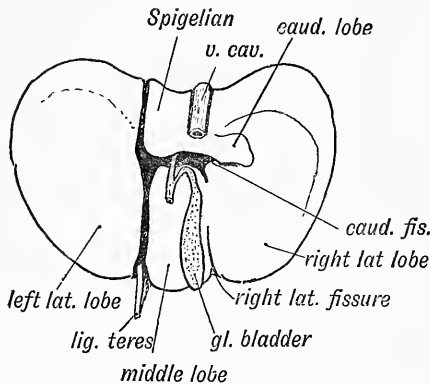


FIG. 290.—The Lower Surface of the Liver of a Human Foetus during the 3rd month, showing Vestiges of Fissures and Lobes of the typical Mammalian Liver.

At birth it occupies nearly half of the abdominal space, and measures $\frac{1}{3}$ th of its final volume. The left lobe may still reach, and even overlap, the spleen. Up to the time of birth nucleated red blood corpuscles multiply within it (page 334). After birth two factors come into operation which lead to a diminution in size and change of shape. It is supplied before birth by placental instead of portal blood; at birth, its blood-forming function ceases; its rate of growth becomes proportionately less than that of other abdominal organs. The stomach, formerly empty, is now filled, and presses the liver towards the right side, causing a change in shape and partial atrophy of the left lobe. Riedel's lobe is a linguiform prolongation of the right lobe below the 10th right costal cartilage caused by compression. It is never present at birth.

The Stomach.—The stomach is developed out of that part of the foregut which lies between the oesophagus and pharynx in front, and the yolk sac, duodenum and liver bud behind. In the 4th week (Fig. 274) it lies in the neck, with the cervical somites dorsal to it, the pericardium

ventral to it, while on each side is the coelomic passage which leads from the pericardial to the peritoneal spaces (Fig. 279). At this time heart, lungs and stomach lie near the exit of the vagal fibres from the central nervous system. During the 6th and 7th weeks, as we have already seen, the growth of the lung buds leads to an elongation of the oesophagus and a backward migration of the stomach which, from being a cervical structure comes to lie level with the lower thoracic segments (Figs. 276, 277). At first its dorsal and ventral mesenteries are undifferentiated from the septum transversum. In the 5th week the gastric part of the fore-gut shows a dorsal bulging—the greater curvature (Fig. 277). As the liver and gut are developed, the stomach separates itself from the septum transversum and comes to be suspended from the dorsal wall of the coelom by the **dorsal mesogastrium** (Fig. 284). The gastro-hepatic omentum is part of the

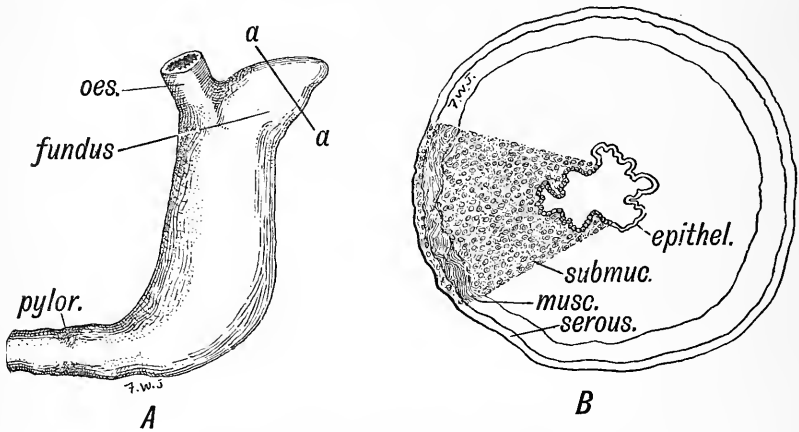


FIG. 291, A.—Stomach of a Human Foetus about the end of the 3rd month, showing the outgrowth of the Fundus of the Stomach. (Wood Jones.)

B.—Section across the Fundus (the line of section is indicated in A), showing the differentiation of the four coats of the Stomach. (Wood Jones.)

ventral mesogastrium. The oesophageal end of the stomach lies between the spinal fibres of the diaphragm which develop in its mesentery; the outgrowth of the liver bud fixes its pyloric end in the ventral mesogastrium. Three changes quickly ensue during the 5th and 6th weeks, the one being partly dependent on the other :

(1) The dorsal border of the stomach, to which the dorsal mesogastrium is attached, grows more rapidly than the ventral border to which the ventral mesogastrium is attached. The **greater** and **lesser curvatures** are thus produced.

(2) The **fundus** of the stomach is produced as an outgrowth from the dorsal border, its origin being similar to that of the caecum from the small intestine (Fig. 291, A).

(3) While the ventral mesogastrium attached to the lesser curvature undergoes a relatively slow growth, the dorsal mesogastrium is affected by a very rapid expansion. Because of the discrepancy in the growth

of these two membranes, the greater curvature of the stomach becomes freely movable, while the lesser curvature remains relatively fixed.

The three factors just enumerated lead to a rotation of the stomach, the greater curvature moving to the left, while the surfaces, formerly right and left, carrying the corresponding vagus nerves, become posterior and anterior. The rotation is already evident at the end of the first month of development (Broman). All of these changes are adaptations to allow the stomach to expand when filled and contract when emptied. As the stomach fills, it is the greater curvature which expands; the lesser curvature remains relatively fixed. By the commencement of the 4th month the stomach is demarcated into a wide, vertical, **cardiac** part, and a narrower

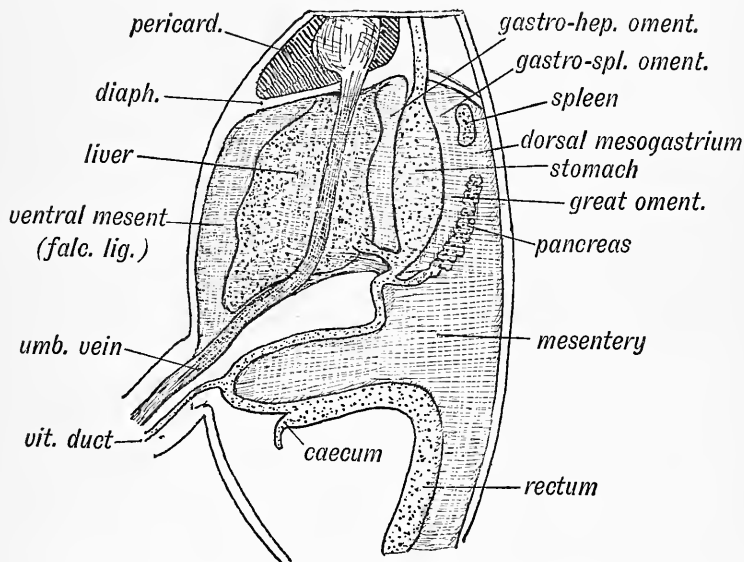


FIG. 292.—The Relationship of the Spleen, Pancreas and Liver to the Mesogastrium in the Embryo.

horizontal or **pyloric** part. The pyloric sphincter becomes differentiated towards the end of the 2nd month, and it is then possible to see a distinction between pylorus and duodenum.

Differentiation of the Coats of the Stomach¹ (Fig. 291, *B*).—A section of the wall of the stomach at the end of the 3rd month of foetal life shows (1) an entodermal lining everywhere showing depressions or pits—the **primary gastric pits**—from which gastric glands will be produced during the 4th month, (2) an extremely thick submucous layer, (3) a circular muscle coat, with nerve fibres and ganglion cells applied to its outer surface; while the circular coat appears during the 7th week, the outer longitudinal coat is not differentiated until the 4th month, and (4) peritoneal coat. From the primary gastric pits solid processes grow within the submucous coat, thus forming the epithelial bases of the gastric glands. Even as late

¹ See reference under Johnson, p. 271.

as the 5th month of foetal life the mucous membrane in the pyloric region has a villous appearance owing to upgrowths between the mouths of the primary gastric pits. True villi, however, commence at the distal border of the pylorus.

The Spleen.—The spleen is formed in the dorsal mesogastrium above the cardiac end of the stomach (Fig. 292) and grows out of the left surface of the mesogastrium (Fig. 293). It appears at the beginning of the 6th week by a localized growth of the mesoderm in the mesogastrium. The thickening becomes vascularized. The coelomic mesothelium, which covers this thickening on the left aspect of the dorsal mesogastrium, rapidly proliferates, the deeper cells invading the vascular basis of the spleen. The tail of the pancreas (Fig. 292) reaches its point of origin. The

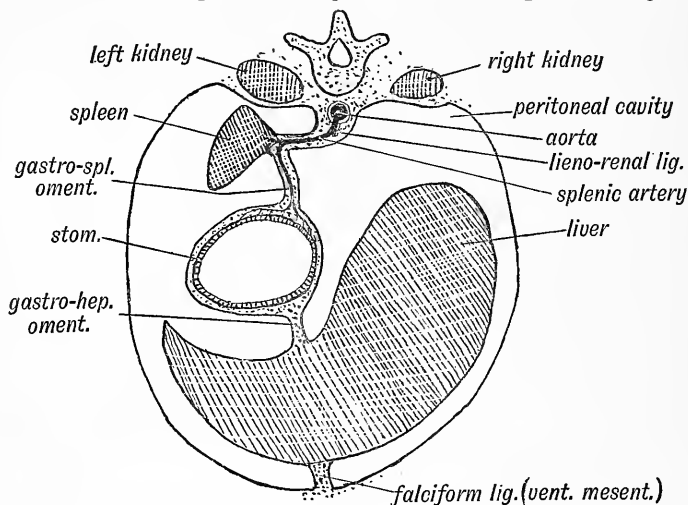


FIG. 293.—A Diagrammatic Transverse Section of the Mesogastrium viewed from behind.

splenic artery is one of the vessels of the mesogastrium (Fig. 293); its branches end in the developing tissues of the spleen and greater curvature of the stomach. The splenic blood spaces are formed during the earlier part of the 3rd month by a dilatation of the capillaries, and perhaps also from veins which, in the developing spleen, are lined by columnar cells. The trabecular and muscular tissues, and the capsule, are derived from the mesoderm of the dorsal mesogastrium. Small masses of splenic tissue (accessory spleens) are occasionally formed in the dorsal mesogastrium near the hilum of the spleen. In lower mammals the splenic formation spreads backwards until it forms a colic lobe lying in the dorsal mesentery of the hind-gut.¹ In the 3rd month the surface of the spleen is nodular and deeply incised; about the middle of foetal life the fissure begins to disappear; only on the anterior or gastric border do they persist. The spleen differs from a lymph gland in that its spaces are formed by dilatations of blood vessels in place of lymph vessels. Lymphoid nodules appear in

¹ W. Colin Mackenzie, *Journ. Anat.* 1917, vol 51, p. 1.

the spleen about the 6th month. The development of the spleen in the mesogastrium and the termination of its blood in the portal circulation suggest that the spleen is concerned in some way with digestion.

The **gastro-splenic omentum** is that part of the dorsal mesogastrium which unites the spleen to the stomach (Figs. 292 and 293). It becomes elongated and stretched as the stomach rotates, and as its greater curvature is developed. The spleen comes to lie against the posterior (right) surface of the cardiac end of the stomach. The dorsal part of the mesogastrium between the roof of the coelom and the spleen becomes the **lieno-renal ligament**. The rotation of the stomach also leads to the spleen being thrust towards the left side; the dorsal or renal surface of the spleen becomes applied to the peritoneum covering the anterior surface of the left kidney and supra-renal body (Fig. 293). The part of the mesogastrium between the spleen and oesophagus adheres to the diaphragm and forms the **lieno-phrenic ligament**. The manner in which the dorsal mesogastrium

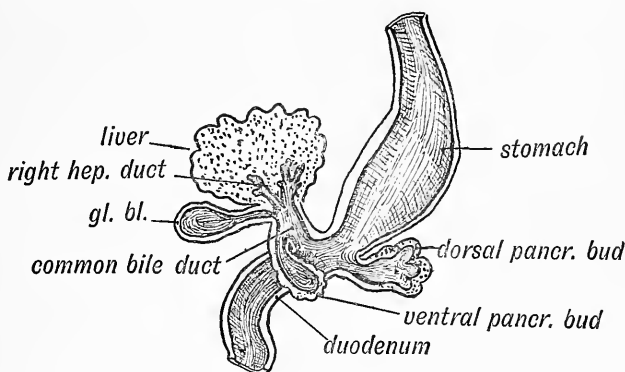


FIG. 294.—The Pancreatic and Hepatic Processes of a 4th week Human Embryo. (After Kollmann.)

becomes applied and adherent to the posterior wall of the abdomen during the 2nd and 3rd months will be described in connection with the secondary attachments of the peritoneum and mesenteries.

The Pancreas.¹—The **Pancreas** appears during the 4th week as two processes from that part of the gut which afterwards becomes the second stage of the duodenum (Fig. 294). The pancreatic buds develop within the ventral as well as within the dorsal mesentery for, at their points of origin from the duodenum, these two mesenteries are continuous (Fig. 292). Of the two buds, one is a minor process which springs from the ventral aspect of the duodenum in common with the hepatic diverticulum. This ventral bud forms only the lower part of the head of the pancreas (Fig. 295). The greater part is formed from a process which springs from the dorsal border of the duodenum, nearer the stomach than the ventral process, and grows into the dorsal mesogastrium above the stomach until

¹ For development of pancreas: F. W. Thyng, *Amer. Journ. Anat.* 1907-8, vol. 7, p. 489; F. T. Lewis, *Keibel and Mall's Manual of Embryology*, 1912, vol. 2, p. 429; Margaret Tribe, *Phil. Trans.* 1913, vol. 208 (B), p. 307; Geo. W. Corner, *Amer. Journ. Anat.* 1914, vol. 16, p. 207.

it reaches the spleen (Figs. 294, 295, 296). A developmental rotation in the wall of the duodenum, brings the bile duct and ventral pancreatic bud in contact with the right or dorsal aspect of the dorsal pancreatic outgrowth. In many animals there are two ventral pancreatic buds, one of which sends a process within the gastrohepatic omentum, round the bile duct, almost to the transverse fissure of the liver. A representative of this omental lobe is occasionally present in man (Fig. 295). The ducts of both processes may persist, the duct of the dorsal bud (duct of Santorini) opening half an inch above the opening of the bile duct; the duct of the ventral bud (Wirsung's) terminates with the common bile duct (Fig. 295). The terminal part of the duct of Santorini commonly becomes obliterated and the secretion of the dorsal pancreatic outgrowth finds a new exit through an anastomosis between its duct system and that of the ventral

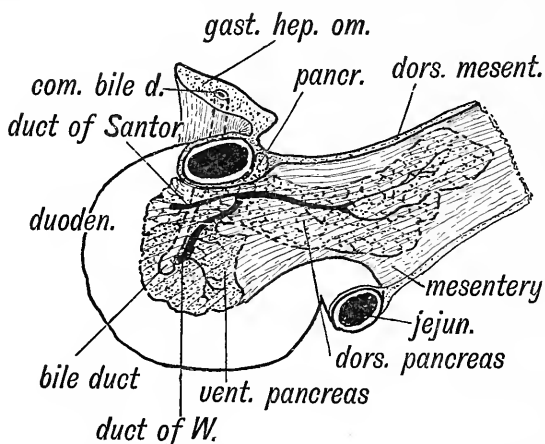


FIG. 295.—Diagram of the Pancreas showing (1) its Primary Relationship to the Dorsal and Ventral Mesenteries; (2) the parts formed from the Ventral and Dorsal Outgrowths; (3) the Formation of the Duct of Wirsung (Duct of W.) by a union between the Ducts of Dorsal and Ventral Buds.

bud, which is effected in the 3rd month. Even if the duct of Santorini persist, the secretion from the dorsal bud reaches the duodenum mostly through the duct of the ventral bud—the duct of Wirsung. Occasionally the duct of Wirsung does not join the common bile duct, but opens separately in the duodenum.

The developing pancreatic process is at first hollow, like the primary liver process, but the secondary outgrowths are solid and cylindrical. They divide and re-divide, acquire lumina, and form an acino-tubular gland. About the end of the 3rd month some of the acini, particularly in the tail of the pancreas, already distinguished by the staining reaction of their cells, become partially or entirely separated from the duct-system and form the **islands of Langerhans**.¹ Rennie, from a study of these in fishes, concludes they are permanent bodies, while the investigations of Dale led him to regard them as temporary in nature, representing resting acini.

¹ K. A. Heiberg, *Ergebnisse der Anat.* 1909, vol. 19, p. 948.

The semi-isolated acini, of which there are several hundreds, are found in all parts of the pancreas, and represent for us the first stage in the separation of an ordinary duct gland into two elements—one connected with an external secretion, the other with a highly important internal secretion. We see from the example of the pancreas how ductless glands like the thyroid and pituitary may have arisen from duct glands by atrophy of the excretory part. The capsule and connective tissue of the pancreas are derived from the mesoderm of the dorsal mesentery.

Relationship of the Pancreas to the Peritoneum and Vessels. 1. **In the Embryo.**—The pancreas develops between the layers of the dorsal mesogastrium, just where this structure is being expanded to form the wall of the omental sac. From the first it is completely surrounded by peritoneum, and it lies with its tail directed forwards against the spleen and its head on the dorsal bend of the **duodenal loop** (Fig. 296). It comes to lie parallel to the great curvature (dorsal border) of the stomach. In Fig. 296 a schematic drawing is given of the essential relationship of the pancreas to the dorsal mesogastrium in lower vertebrate animals; it also represents the condition seen in a human embryo in the 5th week of development, when the dorsal mesentery is swollen with young tissue (Fig. 281) and attached along the mid-dorsal line. The coeliac axis (Fig. 296) is the artery of the mesogastrium and of the structures which it contains. It supplies the fore-gut and its derivatives, between the septum transversum in front and yolk sac behind. The coronary artery passes direct to the cardiac end of the stomach; the splenic is a short vessel ending on the cardiac dilatation of the stomach and supplying the spleen; the hepatic passes on the right side of the pancreas to the duodenum and pyloric end of the stomach, and ends in the liver by passing through the ventral mesentery. As the stomach migrates backwards during the 6th and 7th weeks, the origin of the coeliac axis moves also.

2. **In the Adult.**—The development of the great omentum and the rotation of the stomach to the left, lead to the pancreas being pressed against the left side of the posterior wall of the abdomen. That part of the dorsal mesogastrium which lies between the stomach and pancreas becomes elongated enormously, during the 3rd and 4th months, to form the **great omentum**, and hence the two anterior layers of the great omentum are attached to the great curvature of the stomach and to the gastro-splenic omentum (Fig. 296). The two posterior layers of the omentum end on the lower (formerly ventral) border of the pancreas. The great omentum is well developed in all mammals, its origin being probably related to that of the diaphragm. Its exact function is unknown, but it is connected with the absorption, and perhaps also with the secretion, of peritoneal fluids; it is a great phagocytic mechanism. The duodenal loop, with the head of the pancreas in its concavity, is also pressed against the posterior abdominal wall. During all the changes which take place in the position of the pancreas and spleen, owing to the rotation of the stomach and intestine, one structure remains fixed, and that is the coeliac axis. The part of the mesogastrium in which the spleen and tail of the pancreas are situated becomes greatly drawn out. Both structures,

instead of being situated near the middle line dorsal to the stomach, come to occupy a situation in front of the left kidney, the pancreas thus coming to lie across, instead of along, the abdominal cavity. The mesogastrium is ballooned out towards the left side to form the lesser sac of the peritoneum, and as the splenic artery lies in the mesogastrium it also is drawn towards the left, circumventing the lesser sac of the peritoneum (Fig. 297).

Up to the 6th week of embryonic life the pancreas lies between the layers of the dorsal mesogastrium and the extension from these layers which forms the mesentery of the duodenal loop (Figs. 295, 296); thus right and left surfaces are covered by peritoneum. The left surface, which becomes anterior, retains its covering, but during the 6th week the right

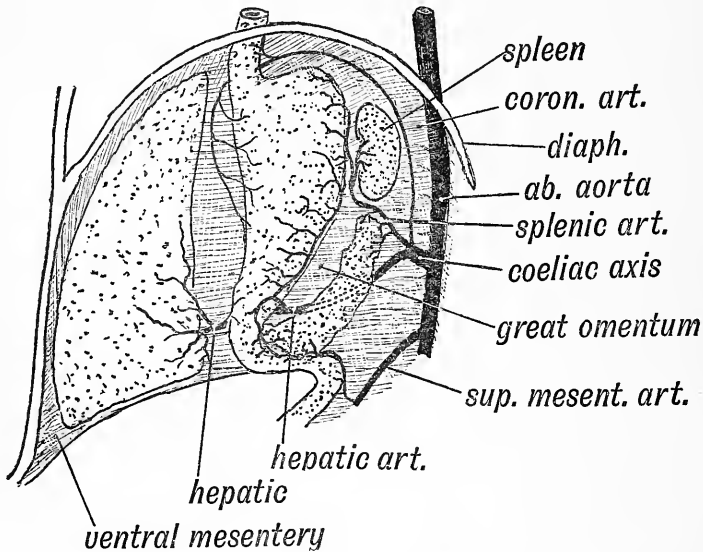


FIG. 296.—Schematic representation of the Dorsal Mesogastrium and its contents.

aspect of the pancreas and duodenal loop become applied to the posterior abdominal wall in front of the aorta, crura of the diaphragm and left kidney (Fig. 297). The peritoneal covering on the right aspect gradually disappears, and thus in the adult the pancreas comes to appear as if it lay behind and outside the cavity of the peritoneum. The complete application and fixation of the pancreas and duodenum to the posterior abdominal wall only occur in animals adapted to the upright posture (see Figs. 287, 288, 297).

The part of the dorsal mesogastrium between the pancreas and aorta (Fig. 297) is also applied to the posterior abdominal wall, and forms the posterior lining of the lesser sac.

The Lesser Sac¹ is composed of two parts, a vestibular or hepatic part formed from the recessus mesentericus (Figs. 287, 288) and an omental or gastric part formed by the evagination of the dorsal mesogastrium.

¹ For fuller details see P. T. Crymble, *Journ. Anat.* 1913, vol. 47, p. 207.

These two parts communicate at an isthmus or constriction caused by the coronary and hepatic arteries (Fig. 297). The hepatic recess or pocket separates the Spigelian lobe of the liver from the right crus, and permits the liver to glide during the respiratory movements of the diaphragm (Figs. 286, 288). The gastric part isolates the stomach, allows it to contract, expand and move during digestion and respiration. In the anterior wall of the lesser sac are situated (Fig. 297) : (1) the gastro-hepatic omentum or ventral mesentery, which is at first vertical and median ; (2) the stomach ; (3) the gastro-splenic omentum, a part of the dorsal mesentery ; (4) the two anterior layers of the great omentum, also parts of the dorsal mesentery. In its posterior wall are situated : (1) the lieno-renal ligament

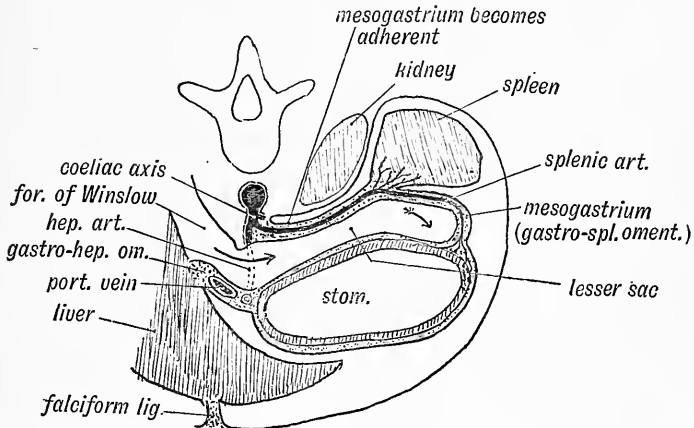


FIG. 297.—Diagram to show the Formation of the Lesser Sac of the Peritoneum from the Dorsal Mesogastrium. The arrow lies in the isthmus between the vestibular and omental parts.

(dorsal mesentery) ; (2) the dorsal mesentery of pancreas ; (3) two posterior layers of the great omentum.

Process of Peritoneal Fixation.¹—We have seen that certain developmental processes, such as the obliteration of the embryonic clefts of the lip and of the palate, or the union of the medullary folds to enclose the neural tube, are akin to the processes which lead to the union of the lips of a wound made by a surgeon's knife. In the peritoneal cavity we are to see examples of another process with which surgeons are familiar—the formation of adhesions which follow inflammatory disturbances of the peritoneum. The passages which lead from the pericardium to the pleura, from the pleura to the peritoneum and from the peritoneal cavity to the tunica vaginalis of the testes, are closed by the formation of developmental adhesions. The peritoneal adhesions with which surgeons are familiar follow inflammation, but the developmental process—the process of **zygosis**—which leads to the adhesion of the mesentery of the duodenum and part of the mesogastrium to the dorsal wall of the abdomen in the latter part of the 2nd month of embryonic life, are not preceded by inflammatory

¹ See Keith, *Lancet*, 1914, vol. 2, p. 362.

changes, but are the result of growth impulses arising under an unknown stimulus. The process of zygosis is active not only in foetal life but is also to be seen at work at, and even after, birth. The applied peritoneal surfaces become adherent by the proliferation and union of lining cells of the opposed layers of peritoneum. The adhesions as they form, contract and thus draw the various parts of the alimentary canal to their final position, much in the same way as the testes come to be lodged in the scrotum. We are here dealing with growth manifestations utilized for a mechanical purpose. The secondary adhesion of the mesenteries of the abdominal viscera are apparently related to posture; the degree of adhesion is much more extensive in man than any other animal, with the exception of the great anthropoid apes. Man and the anthropoids are distinguished from all other animal forms by the upright posture of their bodies. The peritoneal adhesions which occur from the middle of the 2nd month onwards must be regarded as adaptations to the upright posture. The suspensory ligament of the spleen, the right and left **costo-colic** ligaments, the peritoneal bands passing from gall bladder to the colon or omentum are of the same nature, and are formed by secondary adhesions of the peritoneum in the later months of foetal life.¹

The Mid-gut, Yolk Sac and Meckel's Diverticulum.—The yolk sac reaches its maximum size in the earlier part of the 4th week, when its neck, filling the embryonic umbilicus, extends from the septum transversum in front to the allantois behind (Fig. 274). In the 5th week (Fig. 275) the mid-gut has become a V-shaped tube; the yolk sac, now lying in the umbilical cord, just beginning to be differentiated, is joined to the apex of the mid-gut by a stalk or neck. The condition reached in the 6th week is shown diagrammatically in Fig. 298. The following points are to be noted:

(1) The production of the mid-gut as a **U-shaped loop**. (2) The formation within the umbilical cord of a long neck to the yolk sac—the **vitello-intestinal duct**; Meckel's diverticulum is formed by a persistence of the intra-abdominal part of the canal. Normally the duct becomes occluded, and shrivels up during the 6th week; this is the case in all mammals, but in birds the yolk sac is large at the time of hatching, and part of it always persists as an intestinal diverticulum. (3) The yolk sac, by the constriction of the umbilical orifice and formation of the cord, comes to lie on the placenta where a remnant of it may be found at birth near the implantation of the cord (Fig. 298).

Vessels of the Yolk Sac.—Although at first the yolk sac receives a series of branches from the aorta, by the time of its separation from the mid-gut the number has been reduced to one—the superior mesenteric, which becomes the artery of the U-shaped loop (Fig. 298). Its vein, however, the left vitelline, has no connection with the superior mesenteric vein but, when the U-shaped loop is formed continues its original course and ends in the portal vein at the lower border of the pylorus (Fig. 301). When the vitello-intestinal duct atrophies in the 6th week, the same fate overtakes the vessels of the yolk sac, but they, too, may persist as cords.

¹ For many details connected with the formation of these adhesions see papers by Dr. Douglas G. Reid, *Journ. of Anat. and Physiol.* vols. 1911-1915.

The Umbilical Coelom and Intestinal Loop.—At first the coelom extends into the proximal segment of the umbilical cord and it is within

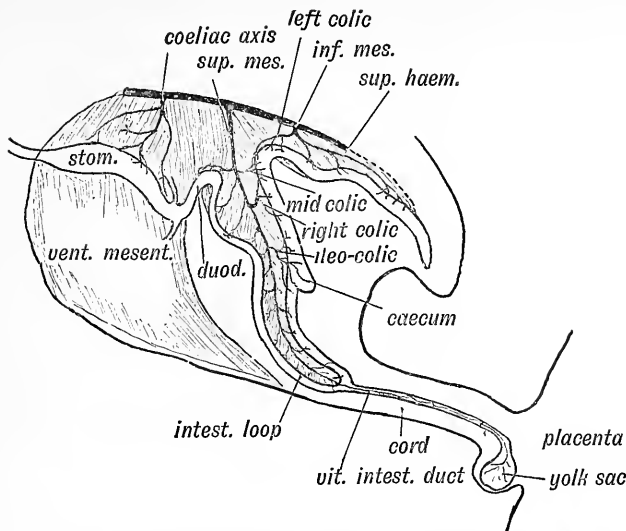


FIG. 298.—Schematic representation of the Alimentary Canal, and of its Mesenteries and Arteries during the 6th week of development.

this umbilical recess of the peritoneal cavity that the U-shaped loop—the mid-gut—undergoes its earlier developmental changes. The structural

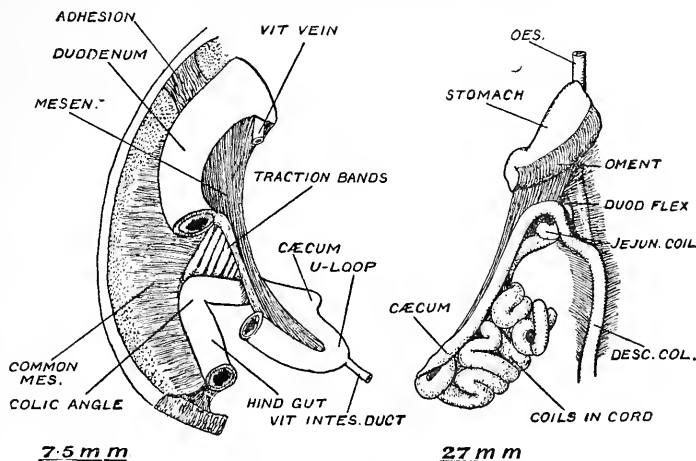


FIG. 299.—The Intestinal Loop, seen from the right side, in an embryo in the 6th week of development. (Prof. Frazer.)

FIG. 300.—The Intestinal Loop, with the Umbilical Coelom, of a foetus in the 9th] week, seen from the left side. (Prof. Bardeen.)

features of the loop are shown in Fig. 298 ; it is made up of a proximal or jejunal limb and of a distal or caecal limb, for already in the 6th week,

when the embryo is little more than 5 mm. in length, the caecal diverticulum is apparent. In Fig. 299 a dissection of the intestinal loop is shown, from an embryo in the 6th week of development. Already the process of rotation has commenced—the jejunal limb coming to lie to the right and dorsal to the caecal limb. The mesoduodenum is becoming adherent to the dorsal wall (Fig. 299) while, as Professor Frazer has shown, certain “traction bands” are forming within the common mesentery and thus guiding and regulating the movement and fixation of the loop. The condition in the 9th week is shown in Fig. 300; within the umbilical coelom coils of small intestine have been produced from the jejunal and ileal parts of the loop; also a jejunal coil within the abdomen from the proximal limb. The duodeno-jejunal flexure has become closely bound to the dorsal wall by traction bands—part of which become muscular and form the **Muscle of Treitz**. Then, suddenly, in the 10th week, when the foetus is about 42 mm. long, the loop is retracted within the abdomen and the umbilical recess becomes closed. We must regard the withdrawal as due to the development of “contraction” or “retraction” bands in the mesentery. During the weeks spent by the intestinal coils in the umbilical recess, the lung buds are expanding and the pleural cavities and diaphragm are being formed, and the safe-guarding of these processes may be the reason for an extra-abdominal development of the intestinal loop.¹

Persistence of Certain Embryonic Structures.²—Many of the structural features seen in the human embryo at the stage of development reached during the fifth or sixth weeks may persist.

(1) The most common structure to remain is the intestinal end of the neck of the yolk sac—**Meckel's diverticulum**. It occurs in 2 per cent. of subjects, and commonly forms a finger-like sac on the free border of the ileum from two to four feet above the ileo-caecal orifice. Hence we know that this part of the ileum forms the apex of the U-shaped loop of intestine. The point on the ileum at which the canal of the yolk sac was attached is frequently the seat of a narrowing, which may be more or less marked. This forms a favourable site at which intussusception of the bowel occurs. The diverticulum varies in length and shape; its blind end is frequently bulbous and the site of secondary diverticula. Occasionally pancreatic masses are developed at its extremity. It is lined by a glandular epithelium similar to that of the ileum. Frequently a fold of the mesentery descends to it (Fig. 302). In the mesenteric fold there is usually to be found a vestige of the artery of the yolk sac (Fig. 298). The attached base of the mesenteric fold may atrophy, while the free margin forms a cord, under which a loop of bowel may become strangulated (Fig. 302).

(2) The vitello-intestinal duct may remain patent, and, when the cord is cut at birth, form a fistulous opening at the umbilicus, by which the

¹ For further details see articles by Frazer and Robbins, *Journ. Anat.* 1916, vol. 50, p. 75; C. R. Bardeen, *Amer. Journ. Anat.* 1914, vol. 16, p. 427.

² For an account of the structure of the yolk-sac see papers by Dr. H. E. Jordan, *Anat. Anzeiger*, 1907, vol. 31, p. 291; 1910, vol. 37, p. 56. For an account of Meckel's diverticulum and of malformations of the bowel see Keith, *Brit. Med. Journ.* 1910, vol. 1, p. 301; Ivar Broman, *Ergebnisse Anat. Entw.* 1913, vol. 21, p. 99.

contents of the ileum escape. Or part may become grafted on the umbilicus and give rise to a "weeping navel" (Stiles).

(3) The artery of the yolk sac, the terminal part of the superior mesenteric, may persist as a fibrous band which stretches from the mesentery at the situation of a Meckel's diverticulum to the umbilicus. Over it the gut may become strangulated. The young of all carnivora are born with thread-like remains of both artery and vein, stretching from the umbilicus to the mesentery (Fig. 301). A remnant of the vein is rarely seen in the human subject. The vitello-intestinal duct may also be reduced to a fibrous structure, over which a loop of intestine may fall and thus become strangulated.

(4) The U-shaped loop, instead of retreating within the abdomen at the beginning of the third month, may remain within the umbilical recess. This gives rise to a **congenital umbilical hernia**. Such herniae occur in all degrees; they may contain a piece of intestine, or almost the whole of the

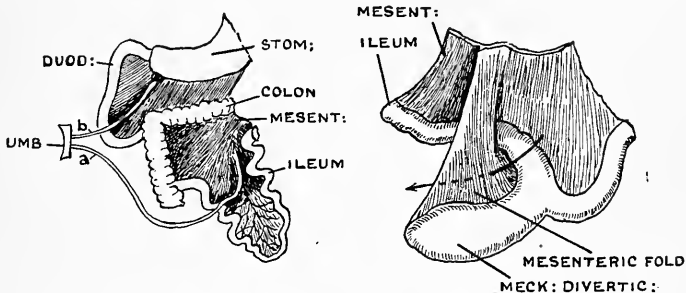


FIG. 301.—Fibrous Remnants of the Artery (*a*) and Vein (*b*) of the Yolk Sac in a Kitten.

FIG. 302.—Meckel's Diverticulum provided with a Mesentery. The arrow marks the site at which an aperture may be formed in the mesenteric fold.

abdominal contents. In such cases the somatopleure, or belly wall, which forms the covering of the hernia, is commonly thin and transparent.

Congenital Diverticula.¹—During the third month numerous out-growths of intestinal epithelium are formed, which perforate the muscular coat. They usually disappear, but may give rise to diverticula, a common site being the ileo-caecal junction where a diverticulum may develop into a large cyst. Frequently masses of pancreatic tissue are attached to intestinal diverticula (Lewis and Thyng).

Congenital Occlusion of the Duodenum.²—The part of the duodenum just above the opening of the bile ducts may be partially or completely closed—a rare occurrence (Fig. 303). After the liver and pancreatic buds grow out, this part of the duodenum becomes occluded by the proliferation of the epithelium lining the gut (Tandler). We have seen that a rotatory

¹ For literature on congenital diverticula see F. T. Lewis and F. W. Thyng, *Amer. Journ. Anat.* 1907-8, vol. 7, p. 505.

² For congenital occlusions see H. Forssner, *Anat. Hefte*, 1907, vol. 34, p. 1; C. P. G. Wakeley, *Journ. Anat.* 1917, vol. 51, p. 65; R. J. Gladstone, *Journ. Anat.* 1914, vol. 48, p. 47.

movement occurs at this site (p. 273). The proliferation of the intestinal epithelium—in the second month—is not confined to the duodenum; hence congenital occlusions may occur at any part of the intestine.

Duodeno-jejunal Loop and Junction.—The junction between the duodenal and U-shaped loops becomes the most fixed point in the whole intestinal tract (Fig. 298). Within its dorsal mesentery a band of non-striated fibres is developed which binds the junction to the right crus of the diaphragm. The **suspensory band**¹ is generally known as the muscle of Treitz. The functional meaning of the duodeno-jejunal loop and its muscular band is unknown, but they are found in all the higher vertebrates (see p. 290).

Villi of the Intestine.²—As early as the 7th week circular muscle fibres appear in the coat of the duodenum and by the 10th week the process has

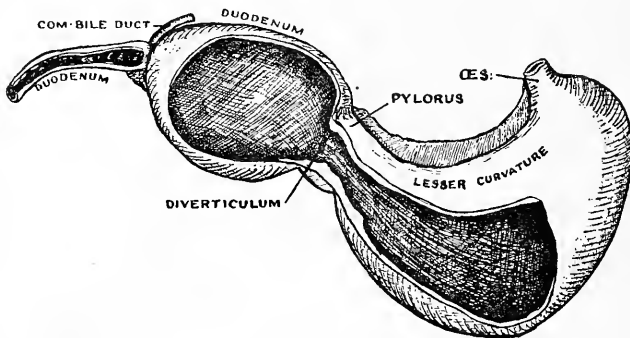


FIG. 303.—Congenital Occlusion of the Duodenum.

spread downwards to the ileo-caecal junction. The longitudinal coat appears in the 12th week and a little later meconium is being propelled towards the great intestine. A germinal zone is formed between the circular and longitudinal coats, in which Auerbach's plexus become developed. Villi begin to form at the end of the second month while the glands of Lieberkühn appear in the 3rd month, both structures being developed in the proximal part first and spreading downwards. The villi arise by subdivision of the ridges (Berry). Lymphoid follicles make an appearance in the 4th month and Peyer's patches begin to form in the 7th month, and are apparent to the naked eye in the 1st month after birth. The **valvulae conniventes** arise as folds of the mucous membrane in the 8th month, thus increasing the surface for absorption. They are formed first in the duodenum; their development gradually ceases at the upper part of the ileum.

¹ A. Low, *Journ. Anat. and Physiol.* 1908, vol. 42, p. 93; P. T. Crymble, *Brit. Med. Journ.* 1910, vol. 2, p. 1156.

² W. A. Hilton, *Amer. Journ. Anat.* 1901-2, vol. 1, p. 459 (Dev. of Villi and Valvulae Conniventes).

DERIVATES OF THE HIND-GUT.

At the beginning of the 2nd month the hind-gut is almost equal in length to the mid-gut, but its calibre is less. Indeed, it is not until the 5th month that the hind-gut is marked off from the mid-gut by its greater diameter. By the end of the 2nd month, as we have just seen, the anterior (jejunal) limb of the intestinal loop has grown very rapidly, and become thrown into a number of distinct loops. At birth the small intestine is six times the length of the large bowel.

The Rectum is formed out of the posterior end of the hind-gut. The manner in which the rectum is separated from the cloaca, the anal canal formed, and the permanent anus produced, will be described in connection

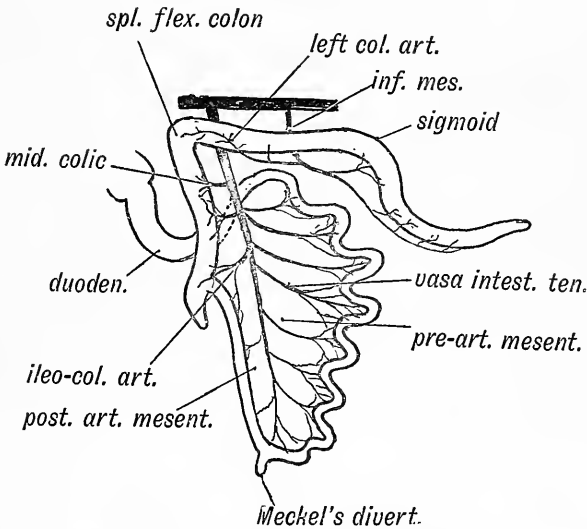


FIG. 304.—The Mesentery of the Hind-gut. The position assumed by the colon after the rotation of the gut has taken place.

with the perineum and urogenital passages, for their history is closely associated with the development of these structures (see p. 381).

The Descending Iliac and Pelvic Segments of the Colon are also formed out of the hind-gut. The artery of the hind-gut is the inferior mesenteric (Fig. 304). Hence it supplies the rectum, sigmoid and descending colon. In the 6th week the hind-gut is suspended from the front of the aorta and spine by the dorsal mesentery of the hind-gut (Figs. 298, 299). This becomes transformed into the meso-rectum, meso-sigmoid and descending meso-colon. The angle between the hind-gut and U-shaped loop becomes the splenic flexure (Figs. 299, 304). At the commencement of the third month, when the intestine takes up its permanent position within the abdomen, the U-shaped loop has become twisted round on the axis of the superior mesenteric artery (Fig. 304), so that the part of the hind-gut which forms the splenic flexure is turned forwards and to the left until it touches

the spleen (Fig. 310). It carries its artery, the left colic, with it. At this time the anterior limb of the U-loop elongates much more rapidly

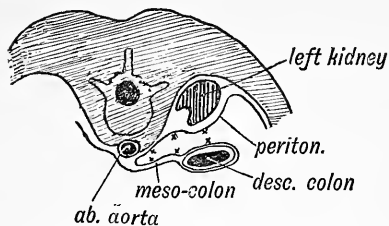


FIG. 305.—Diagram to show how the descending Meso-colon becomes applied to the Parietal Peritoneum of the left Lumbar Region.

than the posterior limb, and is produced into coils of small intestine—the jejunum and ileum—which press the descending meso-colon against the kidney and the parietal peritoneum covering the left kidney (Fig. 305). The left surface and layer of the meso-colon adheres by the process of zygosis to the pre-renal layer of the peritoneum, both layers subsequently being

absorbed. Thus the descending meso-colon, originally situated in the middle line, comes to be attached in the left lumbar region.

The Intersigmoid Fossa.—The sigmoid flexure, which is made up of the pelvic colon and part of the iliac segment, after the rotation of the gut, forms a loop, with its convexity directed towards the liver. The meso-sigmoid is originally attached in the middle line, but the pressure of the developing loop of small bowel presses it against the posterior abdominal wall and left iliac fossa. It may become completely adherent like the descending meso-colon, or only partially. When the sigmoid is lifted up a recess or fossa may be apparent beneath the meso-sigmoid, to the outer side of the left common iliac artery, which is due to a failure of adhesion between the meso-sigmoid and parietal peritoneum. It occurs opposite the convexity of the sigmoid loop (Fig. 288). At birth the meso-sigmoid is relatively extensive; the sigmoid loop lies with its convexity towards the right side of the abdomen, and well above the pelvis. During adolescence the sigmoid grows more slowly than the rest of the colon. It sinks within the pelvis, and forms the greater part of the pelvic colon.

Morphology of the Ileo-colic Part of the Bowel.¹—In all vertebrates, from fishes upwards, the junction of the small with the great intestine is demarcated by the **ileo-colic sphincter**, developed from the circular coat of the bowel.² As a rare abnormality the caecum may be absent in man, the only external indication of the ileo-colic junction being the presence of the ileo-colic sphincter. This is the normal condition in the frog, and in several mammals such as the racoon. The sphincter marks the junction of two different functional segments of the alimentary tract. Villi, which are originally developed in the great bowel, disappear in the

¹For literature on shape and development of caecum and appendix see R. J. A. Berry and L. A. H. Lack, *Journ. Anat. and Physiol.* 1906, vol. 40, p. 247 (Nature of Appendix); F. G. Parsons, *Journ. Anat. and Physiol.* 1908, vol. 42, p. 30 (Age Changes in Shape of Caecum); R. J. A. Berry, "Intercolon," *Med. Journ. Australia*, 1907, June 20 (Nature of Appendix); G. S. Huntingdon, *The Anatomy of the Human Peritoneum and Abdominal Cavity*, 1903; H. A. Kelly and E. Hurdon, *The Vermiform Appendix and its Diseases*, 1905.

²Keith, "Anatomical Evidence as to the Nature of the Caecum and Appendix," *Proc. Anat. Soc.* Nov. 1903. See also Prof. T. B. Johnston, *Journ. Anat.* 1920, vol. 54, p. 67.

later months of foetal life. The proximal part of the colon from which the caecum is developed forms the caecal colon (Fig. 306); it is frequently demarcated from the ascending colon by a thickening of the circular muscular coat—the **caeco-colic sphincter** (Fig. 306), *c*—which can commonly be recognized in the bowel of man. The caecum is developed as a diverticulum of the caecal colon. In all vertebrates its submucous coat is rich in lymphocytes, which in mammals collect in the form of solitary follicles more or less closely crowded together. R. J. Berry found that in the primates there is a tendency for the lymphoid tissue to be aggregated in the apex of the caecum. In man, in anthropoids, and a few other forms, the lymphoid tissue becomes richly developed in the distal part of the caecum, which has a narrow lumen, strong muscular coat, and is of great functional activity during digestion. This highly specialized part of the

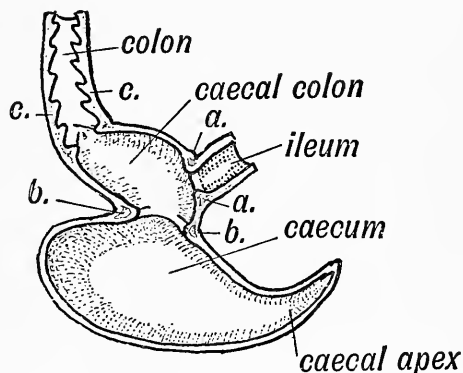


FIG. 306.—Diagram to show the parts of a typical Mammalian Caecum. Five parts are shown in the figure: (1) the termination of the ileum; (2) the caecal colon in which the ileum ends; (3) the caecum which opens from the ascending colon; (4) the apex of the caecum; (5) the commencement of the ascending colon. At three points the circular muscular fibres are thickened to form sphincters: (*a*) ileo-colic junction; (*b*) at the junction of caecum and caecal colon (in man *a* and *b* are combined in the ileo-caecal orifice and its retinacula); (*c*) in the first part of the ascending colon.

caecum is the appendix; it is well developed in man, and is certainly not a vestigial structure. The lymphoid tissue undergoes a great reduction in size and growth when the period of adolescence is past. Thus there are five structures to be observed in the ileo-colic region of a typical mammal (Fig. 306): (1) an ileo-colic sphincter, (2) a caeco-colic sphincter, (3) a caecal segment of the colon, (4) a caecum, the distal part of which may be specialized to form (5) an appendix. Further, a study of the comparative anatomy of this region shows that the caecum is largest in vegetable-feeding animals, and that there is a correlation between the development of the stomach and caecum. In the horse, for instance, the caecum and caecal colon are complicated, the stomach simple; in the ruminants the stomach is complex, the caecum comparatively simple. In animals which live on a flesh diet the caecum is small.

Development of the Colon and Caecum.—Early in the 6th week of development an elevation appears on the free border of the posterior

limb of the U-shaped loop (Figs. 298, 299). The elevation contains a diverticulum of the caecal colon, which forms the caecum and appendix. It continues to grow outwards and forwards in close contact with the free border of the ileum. At first the colic part of the intestinal loop and the caecal process are not of larger calibre than the small intestine, but in the fifth month the colon and caecum undergo an enlargement, but the terminal or apical part of the caecum retains its foetal dimensions, and forms the appendix. As in the small bowel the circular coat appears long before the longitudinal, but whereas the muscle appears first at the proximal end of the small bowel and spreads distally, the muscle of the colon appears first at the rectal end—where the sacral visceral nerves enter—and spreads towards the ileo-caecal junction. The longitudinal coat appears in the 3rd month along the mesenteric border—representing the mesenteric

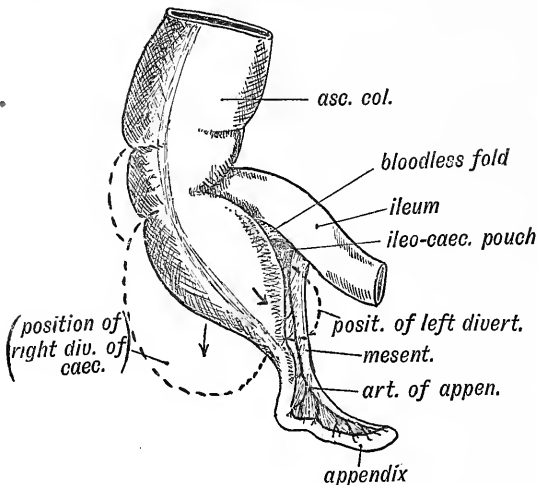


FIG. 307.—Diagram of the Apex of the Caecum at the time of Birth and the Diverticula which may be produced later in the Fundus of the Caecum.

taenia; the remaining two in the 4th month. The evaginations or haustra are distinct in the 7th month of foetal life.¹

As the superior mesenteric (vitelline) artery descends in the intestinal loop, it gives off three branches to the posterior limb—the middle colic, right colic and ileo-colic arteries (Figs. 304, 308). The mesentery of the U-shaped loop may be divided into two parts, the fate of the two parts being different:

1. The mesentery of the anterior limb in front of the superior mesenteric artery—forms the **pre-arterial part**. This gives rise to the greater part of the mesentery of the small bowel.

2. The mesentery of the posterior limb, behind the artery—is the **post-arterial part**. It forms the mesentery of the ascending and transverse colon, and also the lower part of the mesentery of the small bowel.

¹ See Th. Thaysen, *Anat. Hefte*, 1916, vol. 54, p. 321; P. E. Lineback, *Anat. Rec.* 1919, vol. 16, p. 155; E. J. Carey, *Anat. Rec.* 1920, vol. 18, p. 224.

When the rotation of the intestinal loop takes place (p. 289) the splenic flexure of the colon comes against the spleen, while the transverse meso-colon, containing the middle colic artery, is brought into apposition with that part of the mesogastrium which forms the great omentum (Figs. 300, 310). These two layers adhere; thus the transverse colon is formed by the fusion of a part of the dorsal mesogastrium with the mesentery of the posterior limb of the U-shaped loop (Fig. 288). The rotation places that part of the loop mesentery which forms the mesentery of the caecum and ascending colon against the duodenum, and at the same time the duodenal loop becomes fixed in its permanent position in front of the right kidney and inferior vena cava. The caecum thus comes to be situated in the majority of foetuses in front of the right kidney, near the gall-bladder, and there it remains until about the time of birth, when the ascending colon elongates and the caecum thus moves towards the right iliac fossa. An iliac position of the caecum is a feature which occurs only in animals adapted to the upright posture. Thus the attachment of the ascending meso-colon is effected by secondary adhesions which are formed during the migration of the colon and caecum. The appendix, during the migration, may be caught behind the colon, thus assuming a **retro-colic position**; it is then lodged and fixed in the ascending meso-colon. The peritoneal adhesions, which are formed in the 4th and 5th months of foetal life, between the transverse meso-colon and great omentum, and especially the adhesions which the ascending colon forms just before and after birth, as the caecum assumes its position in the iliac fossa, are subject to a great range of variations, and many peritoneal folds and recesses may be formed. The object of all of them is to give a fixation of the viscera to the abdominal wall—a fixation which occurs only in orthograde primates.¹

The Appendix.—At first, and until the fifth month, the caecal diverticulum is of the same calibre throughout, but from that month onwards,

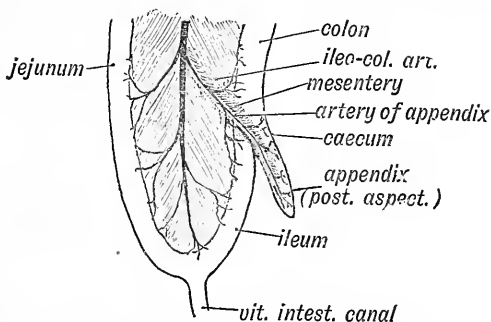


FIG. 308.—The Appendix and Peritoneal Folds at the end of the 2nd month of Foetal Life. The intestinal loop is viewed on its left, later its dorsal, aspect.

the appendix remains small while the caecum grows, keeping pace in diameter with the colon. At birth the appendix is still the tapered apex of the caecal diverticulum (Fig. 307), but during childhood, an outer, or an

¹ Dr. Douglas Reid has described the various forms of foetal adhesions in *Journal of Anatomy and Physiology*, vols. 1911-1915.

inner sacculation, or both together, arise in the fundus of the caecum and thrust the appendix backwards and to the left into an asymmetrical position.¹ Villi are formed in the mucous coat in the early part of the 4th month; Lieberkühn's glands appear a little later. Lymphoid follicles make their appearance in the 5th month. The villi disappear in the 8th month.

Although a distinctly marked appendix is only seen in man, the anthroids, lemur, opossum and certain rodents, still a corresponding lymphoid structure is present generally in mammals. The appendix is a lymphoid diverticulum of the caecal apex (R. J. Berry). It must be regarded as a lymphoid structure, and although it can be dispensed with, is not therefore to be regarded as vestigial in nature any more than is the tonsil. In 30 % of adults both muscular and mucous coats have undergone a partial degeneration under modern conditions of diet, and the appendix does tend to become a useless structure.

Ileo-caecal Valves.—At the ileo-colic junction, the development of villi ends. In the higher primates the junction is invaginated within the caecum, in the form of two lips or valves. The invagination becomes apparent in the human foetus of the 3rd month. Within these folds are (1) the ileo-colic sphincter; (2) muscular bands developed in the **retinacula** from the circular musculature of the caecum and representing the **mid-caecal** sphincter of the typical caecum (Fig. 306). The retinacular musculature assists in the emptying and filling of the caecum. To a very slight extent the ileo-colic lips can serve as mechanical valves in the living subject; they assume a valvular form only when dead and dried.

Ileo-caecal Fossae.—When the caecal diverticulum grows out from the hinder limb of the U-shaped loop it carries with it three folds (see Fig. 309):

1. **The ileo-colic fold**, a process from the right side of the mesentery containing the anterior caecal artery; in a small proportion of cases this fold forms the mesentery of the appendix;²

2. **The bloodless or ileo-caecal fold**, a process from the coat of the ileum;

3. **The mesentery of the appendix**, a process from the left side of the mesentery, containing the artery to the appendix (Fig. 308).

These three folds give rise to three **fossae** (Fig. 309):

1. **The ileo-colic**, between the termination of ileum and ileo-colic fold;
2. **The ileo-caecal**, between the bloodless fold and mesentery of the appendix; 3. **The retro-caecal**, between the mesentery of the appendix and commencement of the ascending meso-colon.

The caecum and appendix are made up of bilateral halves; there are right (anterior caecal fold) and left (mesentery of appendix) mesenteries. In birds the appendix is divided; it is occasionally double in malformed human infants.³ There is no reason to suppose, however, that the appendix was ever a double structure in the stem from which man has descended.

The duodeno-jejunal fossa is formed to the left of the duodeno-jejunal flexure after the transverse colon and caecum have rotated to the right

¹ See F. G. Parsons, *Journ. Anat. and Physiol.* 1908, vol. 42, p. 30.

² See Dr. Geo. M. Smith, *Anat. Record*, 1911, vol. 5, p. 549; A. Forster, *Anat. Hefte*, 1918, vol. 56, p. 5.

³ Dr. F. Wood Jones, *Journ. Anat. and Physiol.* 1912, vol. 46, p. 193.

hypochondrium and when the transverse meso-colon has fused with the omental layers of the lesser sac (Fig. 310). The fossa is occupied by a bend of intestine at the duodeno-jejunal junction and serves as a bursa

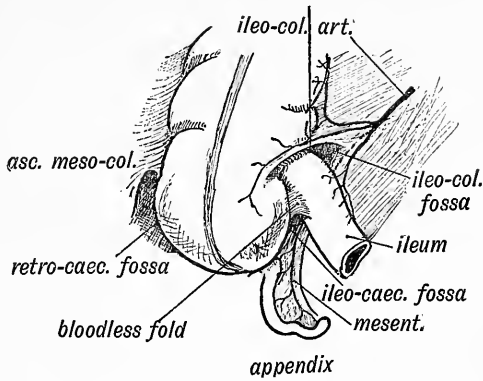


FIG. 309.—Peritoneal Fossae in the Ileo-caecal Region.

for this knuckle of gut. Its origin is connected with (1) the traction bands developed at this junction (see p. 290), the passage of the inferior mesenteric vein in or near its left border. It lies in the axis at which the mesenteric rotation takes place (Fig. 310), and when the plastic nature of

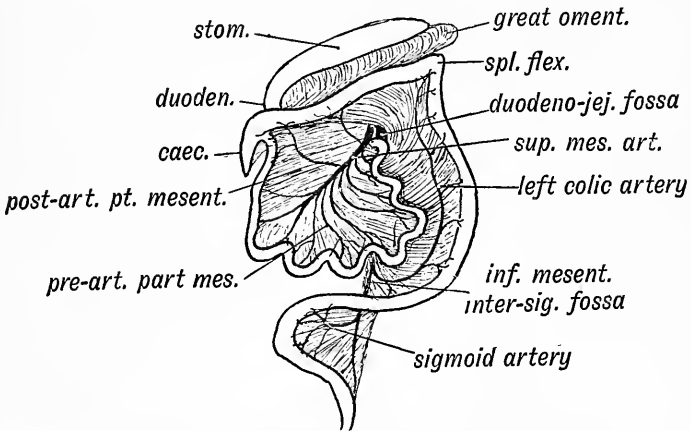


FIG. 310.—To show the Rotation of the Intestinal Loop and Formation of the Duodeno-jejunal Fossa.

the peritoneal tissue is remembered, it is easy to realize how this and other recesses may be formed near the termination of the duodenum.

The mesentery of the small gut is formed out of the primitive mesentery of the U-shaped intestinal loop, chiefly from that part of it (the pre-arterial) which lies between the superior mesenteric artery and the anterior limb of the loop (Fig. 304). After the rotation, the aspect of the mesentery, which was directed towards the right, becomes left and anterior (compare

Figs. 298, 310). During the rotation of the gut the superior mesenteric artery comes to lie in front of the third stage of the duodenum. At first the mesentery is attached in front of the spine only at the origin of the superior mesenteric artery (see Figs. 287, 288). Its oblique attachment to the posterior abdominal wall, from the duodenum to the right iliac fossa, is effected by secondary adhesions which are formed after the rotation of the gut and during the 4th and 5th months, and this extensive attachment is found only in animals adapted to the upright posture. The last part of the mesentery to become adherent to the posterior wall of the abdomen is the angular area between the ileum and ascending colon. Not unfrequently this part remains free, and it is then possible for a **volvulus** to form by a rotation of the ileo-colic loop.

By the rotation of the U-shaped loop, the small intestine becomes confined in a bursa or peritoneal compartment formed by the mesentery of the large bowel (Fig. 310).

Abnormal Fixation of the Mesentery.—The rotation of the bowel is subject to three forms of disturbance, giving rise to three varieties in the fixation of the mesentery, which are of importance to medical men. (1) The bowel may undergo its normal rotation, but the process of adhesion may fail; the bowel is thus suspended by a free fan-shaped mesentery. During life it may become twisted round its stalk, formed by the superior mesenteric artery, and thus give rise to obstruction of the bowel (complete volvulus). (2) It may not undergo a rotation; the caecum then lies on the left side of the abdomen, and the colon—ascending and descending—are situated behind and to the left of the small bowel. (3) The rotation may occur in a direction opposite to the normal—the duodenum and mesentery coming to lie in front of the transverse colon in place of being situated behind it. Several cases of this nature have been recorded of late by surgeons and anatomists.

Meconium.—At birth, the great intestine and the ileum are distended by meconium, a black, semi-fluid substance secreted by the liver and mucous membrane of the bowel. Dr. A. Low found that the meconium reaches the ileo-colic junction in the 4th month, the rectum in the 5th. The meconium passes quickly along the jejunum. At birth the lower part of the ileum and whole of the great intestine are distended with it. By the 3rd or 4th day after birth all the meconium has been passed, a fact which may be utilized to prove that a child had lived for a certain time after birth.

CHAPTER XX.

CIRCULATORY SYSTEM.

Early Stages in the Evolution of the Heart.—In *Ammocetes*, the larval form of the lamprey, is represented the most primitive form of heart in vertebrate animals. Even in this early type the heart consists of four chambers (Fig. 311): (1) Sinus venosus, receiving the portal blood through the liver; (2) auricle; (3) ventricle; (4) bulbus cordis, from which the primitive ventral aorta passes out to distribute the blood in the branchial chamber. The primitive heart is thus a respiratory pump

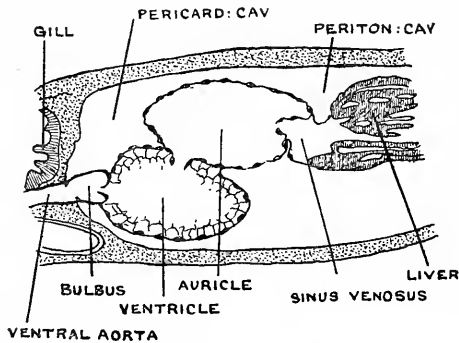


FIG. 311.—The Heart of *Ammocetes* seen in a Median Section. (After Vialleton.)

which forces the portal blood through a branchial system. It is clear, then, that the early evolutionary stages of the heart must be sought for amongst invertebrate forms, but these stages are as yet unknown. When the heart appears in the human embryo towards the end of the 3rd week, it is double—consisting of a right and left cardiac tube. We therefore suppose that originally there were right and left hearts, which arose as modifications of the vessels which convey the blood from the alimentary to the respiratory systems. In Fig. 312 the left side of such a primitive circulation is represented. The left heart forces the blood along a primitive dorsal aorta to the capillary system of the archenteron. An afferent (primitive portal) vessel conveys the blood back to the heart. When the head and tail folds are produced in the embryonic plate at the beginning of the 4th week (see Fig. 312), the right and left cardiac tubes are thrust under the fore-gut, where they speedily become fused into a median

heart.¹ In its origin the heart is thus made up of symmetrical halves derived from the corresponding sides of the body. When formed, the heart is suspended within the anterior part of the coelomic space—which becomes the cavity of the pericardium. In *Ammocetes* the pericardial and peritoneal cavities are continuous (Fig. 311).

Angioblastic Tissue.—That the cardiac tube has arisen by the modification of a blood vessel is apparent by the way it commences to form in the human embryo. Late in the 3rd week certain cells become grouped under the fore-gut to form the lining membrane of the heart. At the same date similar cells in the chorionic villi, in the wall of the yolk sac and along the tracks of the future aortae, are grouping themselves in an identical manner to form the lumina of blood channels. The mesodermal cells which have this vessel-forming power pervade the whole embryonic

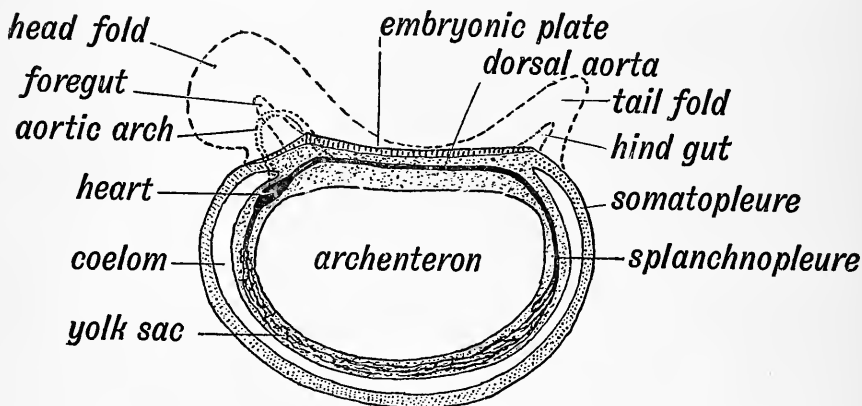


FIG. 312.—Diagram showing the Relationship of the Heart to the Archenteron of the Developing Ovum. The outgrowth of the head fold is indicated carrying a process (fore-gut) of the Archenteron and also the Aorta and Heart. The outgrowth of the tail fold and hind-gut is also shown. (After A. Robinson.)

mass and are known as angioblastic tissue. One group of angioblasts unites with neighbouring groups, thus forming a network. Further, angioblasts not only form the lining cells and lumina of blood vessels but also produce the blood cells and plasma which fill them. A "blood island" is a group of angioblasts surrounding a brood of nucleated red corpuscles. When neighbouring islands unite the essential part of the circulatory system has come into existence. The lining of the heart arises in the same manner as a simple capillary.²

Later Stages in the Evolution of the Heart.—So long as the heart is merely a pump for the gills, it retains the simple structure seen in *Ammocetes*—but with the origin of a pulmonary system a series of most remarkable changes occur. The pulmonary system in the human embryo

¹ Recent papers on fusion of cardiac tubes: Chung-Ching Wang, *Journ. Anat.* 1918, vol. 52, p. 107; H. W. Schulte, *Amer. Journ. Anat.* 1916, vol. 20, p. 45; Henry A. Murray, *Amer. Journ. Anat.* 1919-20, vol. 26, p. 29.

² For recent papers on angioblasts: J. L. Bremer, *Amer. Journ. Anat.* 1914, vol. 16, p. 447; Florence R. Sabin, *Contrib. to Embryology*, 1920, vol. 9, p. 213.

takes on its definite form during the second month; at the same time the heart is undergoing a series of changes, which converts it into a double pump, one for the lungs, another for the body. We know that these evolutionary changes occurred slowly, for in amphibia the heart has reached that point in evolution where a single ventricle can serve both the respiratory and systemic circulations. The evolution of a pulmonary system also led to a series of changes in the arrangements of veins. Amongst the most remarkable of these is the formation of a new passage, by which the blood of the abdomen can pass direct to the heart—the inferior vena cava. In the human embryo of the 5th week the heart and great veins are arranged as in a fish; in the 7th week they take on the definite mammalian form.

Fixation of the Heart.—At the beginning of the 4th week (Fig. 279) the heart lies free within the pericardium, with its two extremities fixed to the wall of that cavity (Figs. 330, 333). Its anterior or arterial extremity

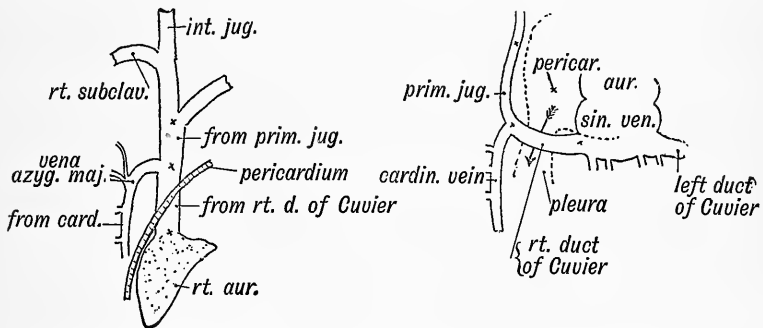


FIG. 313.—The Superior Vena Cava of the Adult.

FIG. 314.—The Embryonic Venous Trunks out of which the Superior Vena Cava is formed. The arrow is in the communication between the pericardial and pleuro-peritoneal cavities. (See Fig. 315.)

perforates the dorsal wall of the pericardium to give off the aortic arches in the floor of the pharynx (Fig. 248). The venous or posterior end is fixed to the septum transversum, the embryonic partition, which is formed between the pericardial and peritoneal cavities (Fig. 279). The fate of the aortic arches, which convey the blood from the ventral to the dorsal aorta, has been already traced (p. 251). We now propose, before surveying the complicated changes which ensue in the heart itself, to trace the evolution of those great venous channels which convey the blood to the heart—the venae cavae.

1. The **superior vena cava** arises from the following foetal vessels (Figs. 313, 314):

(a) The part above the entrance of the vena azygos is the terminal part of the right anterior cardinal (primitive jugular) vein;

(b) The part below the entrance of the vena azygos major represents the right duct of Cuvier. The condition of these venous trunks, the anterior and posterior cardinal veins and ducts of Cuvier, in a human embryo of the 4th week, is shown in Figs. 314, 315. The condition shown in these figures is retained permanently in fishes.

The **anterior cardinal**, which drains the anterior half of the body on each side, with the **posterior cardinal vein**, which drains the posterior half of the body, receive a tributary (segmental vein) from each body segment. In Fig. 315 the anterior and posterior cardinal veins on each side are shown uniting to form the **duct of Cuvier**, which conveys the blood to the sinus venosus—a contractile chamber opening into the primitive auricle. The sinus venosus remains as a separate chamber of the heart in lower vertebrates, but in the course of mammalian development it becomes partly merged in the right auricle of the heart.

It is important to notice how the ducts of Cuvier reach the sinus venosus (see Figs. 315, 330, 280). They pass from the dorsal to the ventral surface of the body in the *somatopleure* or body wall, and enter the **septum trans-**

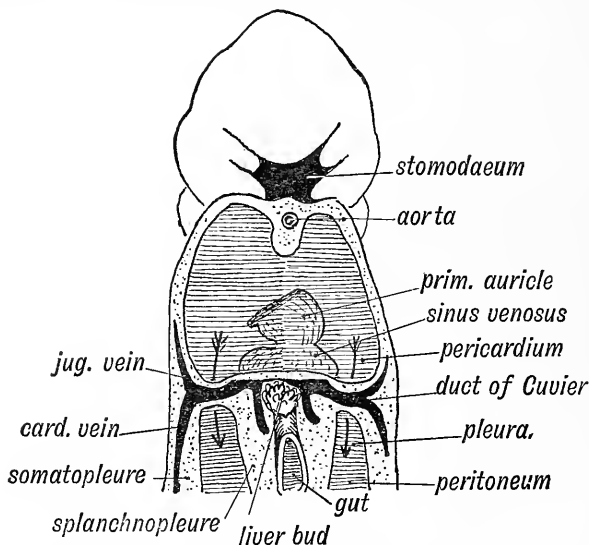


FIG. 315.—Diagram to show the manner in which the Ducts of Cuvier encircle the Coelom at the junction of the Pericardial and Peritoneal Passages at the 4th week. (After His.)

versum to reach the sinus venosus, thus encircling the coelomic passages passing from the pericardial to the pleuro-peritoneal cavities. Thus the exit from the pericardial cavity to the pleural passage is surrounded by the great venous channels—the ducts of Cuvier; hence the exit is sometimes named the **iter venosum** or **pericardio-pleural** passage. Ultimately, by the end of the 6th week, the part of the coelom lying in front of the ducts of Cuvier and septum transversum is cut off from the rest; the part so cut off forms the pericardium. In the 4th week the dorsal end of the septum transversum is situated opposite to the 2nd cervical segment; by the end of the 6th week, the embryo being about 10 mm. long, it has shifted backwards so as to lie on a level with the 3rd thoracic segment, in this way bringing the duct of Cuvier into an oblique position (Fig. 330). Thus the ducts of Cuvier are instrumental in separating the pericardial from the pleural cavity. If the primitive pleuro-pericardial communication

(iter venosum of Lockwood) persists between them, it occurs as a foramen in the pericardium behind the part of the superior vena cava derived from the duct of Cuvier. On the left side the duct of Cuvier atrophies, and the iter venosum, if it persists, is then represented by an aperture in the pericardium in front of the root of the left lung (Fig. 316). The ducts of Cuvier, and the folds of the somatopleure in which they lie, are separated from the body wall and buried deep in the thorax by the development of the lungs and pleurae.

2. **The Vestigial Fold and Oblique Vein of Marshall.**—In the human embryo, during the 4th week, and for two weeks afterwards, there is a right and left duct of Cuvier and corresponding cardinal veins (Fig. 319). A left superior vena cava is present and may persist (Fig. 317). The vestigial fold and oblique vein of Marshall (Fig. 318) are all that usually remain of the left superior vena cava. The right superior vena cava,

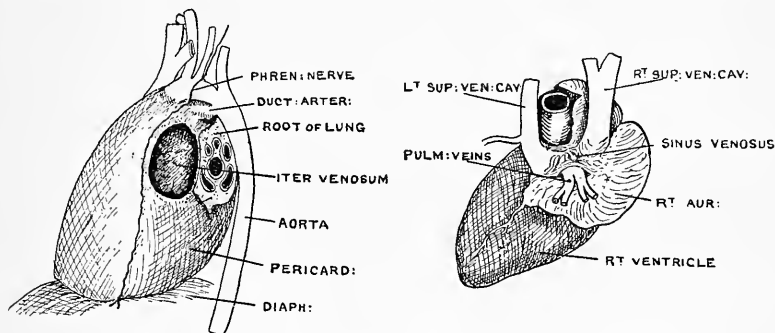


FIG. 316.—Heart of a Child, showing an Abnormal Aperture in the Pericardium in front of the root of the Left Lung, representing a patent Iter Venosum or Pericardio-pleural passage of the Embryo. The left auricle is seen within the aperture.

FIG. 317.—Abnormal Heart of a Child seen from behind, showing Persistence of the Left Duct of Cuvier, absence of the Inferior Vena Cava, and with the Pulmonary Veins terminating in the Sinus Venosus. A similar condition is seen in certain fishes.

within the pericardium, passes in front of the right pulmonary vessels, and is bound to them by a mesentery or fold of serous pericardium; the left has a similar relationship (Fig. 318); when it disappears the pericardial reflection remains in front of the left pulmonary vessels as the vestigial fold. The intra-pericardial part of the left vena cava or duct of Cuvier becomes the oblique vein: it turns round the left auricle to terminate in the left horn of the sinus venosus (coronary sinus). The extra-pericardial part of the left duct of Cuvier joins the superior intercostal vein (Fig. 318). Both right and left superior venae cavae persist in some lower mammals, and occasionally this is also the case in man. The left superior vena cava begins to atrophy when the common auricular chamber is divided into a right and left compartment in the 6th and 7th weeks.

The **left superior intercostal vein** represents the following embryonic vessels (see Fig. 318): (a) Anterior part of the left posterior cardinal vein; (b) The extra-pericardial part of the left duct of Cuvier; (c) The terminal part of the left primitive jugular vein.

3. **Left Innominate Vein** opens up as a channel of communication between the two primitive jugular veins, the left superior vena cava undergoing a simultaneous process of atrophy (Fig. 318).

4. **Subclavian Veins** are developed in the 5th week with the outgrowth of the fore-limb buds; they are developed from the vein of the 7th cervical segment and at first end in the posterior cardinal vein. As the neck and thorax become demarcated in the 2nd month, the termination of the subclavian veins is shifted until it ends in the anterior cardinal (primitive jugular) vein.

5. **Jugular and Cerebral Veins.**—In the 6th week each anterior cardinal vein commences in a corresponding primitive head vein (see page 133). Each primitive head vein passes along the base of the skull, receiving the

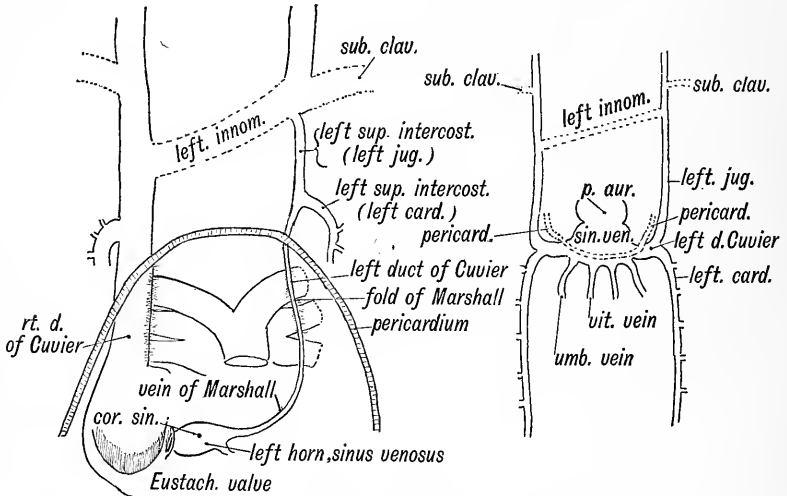


FIG. 318.—The Remnants of the Left Superior Vena Cava, derived from the Structures shown in Fig. 69.

FIG. 319.—Diagram of the Sinus Venosus and Ducts of Cuvier of the Human Embryo about the 4th week.

veins from the fore-, mid- and hind-brains, and makes its exit by the jugular foramen, where it becomes the jugular or anterior cardinal vein.

Posterior Cardinal Veins and their Derivatives.¹—In Figs. 320, 321 a schematic representation of the origin of the inferior vena cava and azygos veins is given. In the 5th week the posterior cardinals commence by the union of the veins from the limb buds and sacrum and passing forwards, dorsal to the developing Wolffian ridge, receive as they go a tributary from each somite—tributaries which will become the lumbar, intercostal and lower cervical veins, and end in the veins of Cuvier. With the development of the nephric or Wolffian system, a large tributary—the **subcardinal** vein—appears on the mesial side of the system or body, collecting blood from and pouring it into the posterior cardinal vein at the

¹ Florence Sabin, *Contrib. Embryology*, 1915, vol. 3, p. 5; Huntington and M'Clure, *Anat. Record*, 1908, vol. 1, p. 36; *ibid.* 1920, vol. 20, p. 1.

cephalic end of the nephric body. Ultimately the subcardinal veins extend their origin in a caudal direction and effect a communication with the hinder part of the posterior cardinal veins (Fig. 320). There is thus established a reno-portal system comparable to that seen in amphibia (Fig. 322). A wide cross channel (internephric) opens between the subcardinals.

From the **right posterior cardinal vein** are formed (1) the vena azygos major; (2) the ascending lumbar vein.

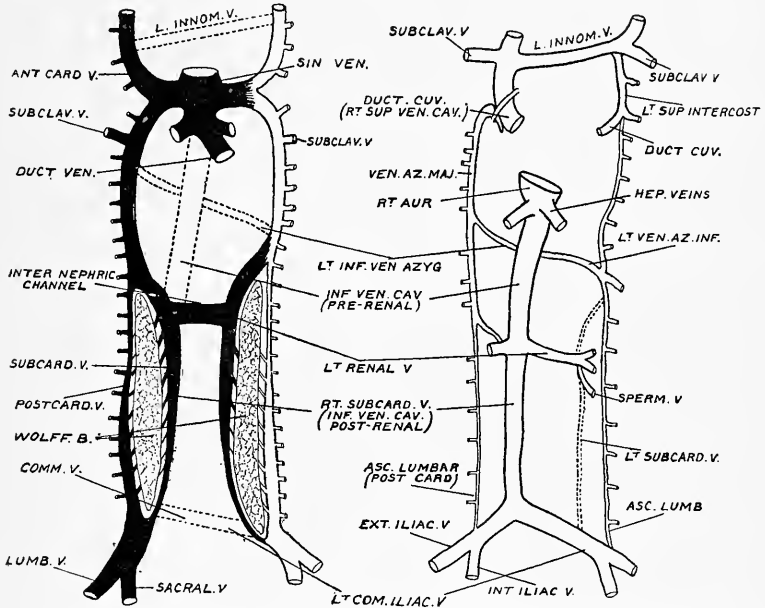


FIG. 320.—Scheme of the arrangement of body veins about the end of the 6th week of development. The sites of new channels are stippled.

FIG. 321.—Scheme showing the derivation of the body veins of the adult.

From the **left cardinal** arise (Figs. 320, 321)—(1) Part of the left superior intercostal vein; (2) left superior azygos vein; (3) left inferior azygos; (4) the left ascending lumbar vein.

Inferior Vena Cava.—The transformation of the cardinal system and the development of a new caval channel to convey the blood in the systemic veins of the abdomen direct to the heart, take place during the 2nd month as the pulmonary system begins to expand. With the evolution of lungs, respiratory movements of the body wall were introduced—a new force which was utilized to assist the return of the venous blood to the heart. The development of pleural cavities made the old or cardinal route circuitous and difficult and hence a new or direct passage became necessary—the inferior vena cava. It became fashioned thus; a retrohepatic anastomosis between the right subcardinal and terminal part of the right vitelline vein (Fig. 320) opened up and thus the blood of the subcardinal system could pass straight to the heart. The pre-renal or retrohepatic part of the

inferior vena cava is formed out of this new channel. The post-renal part is formed from the right subcardinal vein. A cross channel (pre-sacral) opens up between the right and left cardinal systems—forming the greater part of the left common iliac vein—and so all the blood from the pelvis and pelvic limbs passes to the right subcardinal as it becomes converted into a permanent channel. The left subcardinal¹ vein persists not unfrequently—giving rise to a double or **divided inferior vena cava**. The internephric channel becomes the left renal vein, the terminal parts of both subcardinal veins persist as communications between the renal and azygos veins (Fig. 321). From Figs. 320, 321, it will be seen that part of

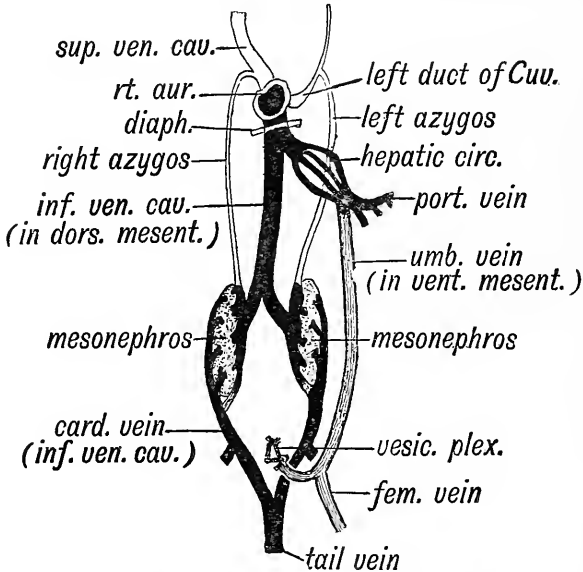


FIG. 322.—The Arrangement of the Cardinal, Umbilical and Inferior Caval Veins in Lower Vertebrates. The venous blood from the posterior part of the body passes through either the renal or hepatic circulations before reaching the heart. (After Hochstetter.)

the common iliac veins are derived from the hinder part of the cardinal system of veins.

Portal Vein.—The **Portal Vein** is formed out of the terminal parts of the two vitelline veins. They end in the posterior chamber of the tubular heart of the embryo—the **sinus venosus**. The vitelline veins, right and left, arise from ramifications on the yolk sac and pass in the ventral mesentery of the fore-gut to the sinus venosus (Fig. 323). The nutriment within the yolk sac is thus carried to the heart and distributed by the heart to the tissues of the embryo and yolk sac. With the differentiation of the gut from the yolk sac, the parts of the vitelline veins, at first situated

¹ For literature and description of cases of abnormal development of the posterior cardinal veins, see Dr. Gladstone's article in *Journ. Anat. and Physiol.* 1912, vol. 46, p. 220; J. Cameron, *ibid.* 1911, vol. 45, p. 416; T. B. Johnston, *ibid.* 1913, vol. 47, p. 235; H. Rischbieth, *ibid.* 1914, vol. 48, p. 290; W. E. Collinge, *ibid.* 1916, vol. 50, p. 235.

on the yolk sac, fuse together in the dorsal mesentery. Thus while the terminal parts of the vitelline veins lie in the ventral mesentery of the fore-gut, the three tributaries of the portal vein—the splenic vein from the fore-gut, the inferior mesenteric from the hind-gut, and the superior mesenteric from the mid-gut (Fig. 323)—lie in the dorsal mesentery. They are developed as tributaries of the vitelline veins, for we have already seen that the veins of the yolk sac may persist as a cord which joins the superior mesenteric vein below the pancreas (see Fig. 301). The duodenum forms a loop between the vitelline veins (Fig. 324), and hence on

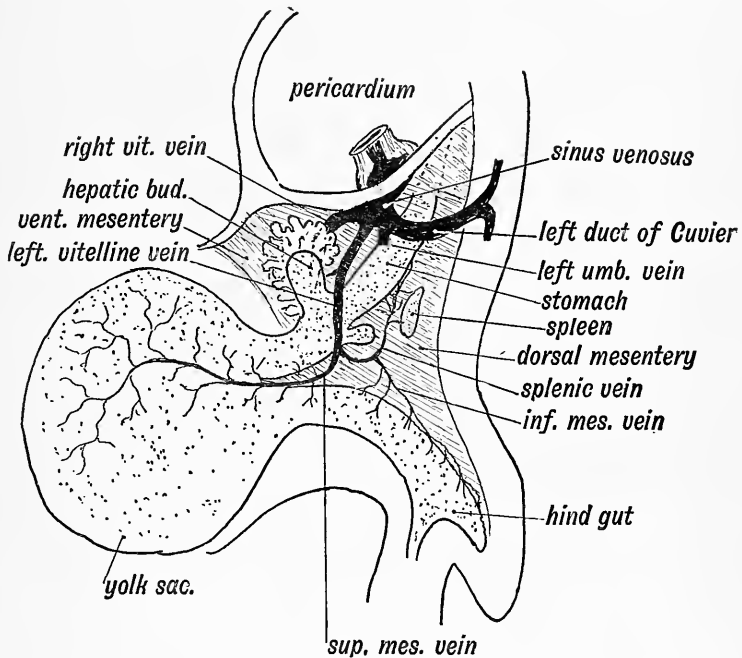


FIG. 323.—The Left Vitelline Vein of an Embryo of the 5th week.

either side of the 1st and 3rd stages of the duodenum the vitelline veins remain separate, while in front, between and behind these stages, they are united by anterior, middle and posterior junctions (see Fig. 324).

The portal sinus in the transverse fissure of the liver is formed out of the anterior junction of the right and left vitelline veins in the ventral mesentery (Figs. 324, 282); the part of the portal vein in the gastro-hepatic omentum (ventral mesentery), and behind the 1st stage of the duodenum, is formed from the right vitelline vein; the corresponding part of the left vein disappears; the commencement of the portal vein—in the neck of the pancreas—represents the middle junction of the two vitelline veins (Fig. 324); the terminal part of the superior mesenteric vein, which in the adult lies in front of the 3rd stage of the duodenum, represents a part of the left vitelline vein—the corresponding part of the right disappears (Fig. 283). To understand the transmutation which

leads to the formation of the portal vein, it must be remembered (1) that the duodenum forms at first a free loop, the right surface of which afterwards becomes applied to the posterior wall of the abdomen; (2) the pancreas is developed in its dorsal mesentery; (3) the ventral mesentery, in which the liver is developed, is attached to the anterior part of the loop (Fig. 323).

Hepatic Veins are formed out of the terminal parts of the vitelline veins. These veins end at first in the sinus venosus (Figs. 282, 283, 324). The liver is developed between and around their terminal parts (see p. 273). Thus it comes about that the vitelline veins are transformed into the

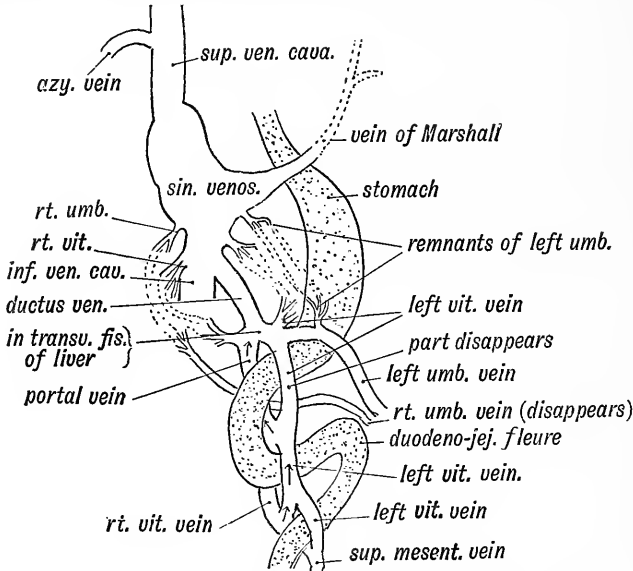


FIG. 324.—Diagram showing the Formation of the Ductus Venosus, and the fate of the Umbilical and Vitelline Veins. The arrows show the parts of the vitelline veins which become the portal vein.

veins of the portal and hepatic circulation. All the foetal and umbilical blood is at first poured through the liver.

Ductus Venosus is a new channel formed in the 5th week between the portal sinus and the terminal part of the right vitelline vein, whereby the greater part of the umbilical blood is short-circuited to the sinus venosus without passing through the liver. After birth, when a short circuit is no longer required between the placental circulation and heart, it becomes reduced to a fibrous cord.¹ It occupies the posterior part of the longitudinal fissure of the liver and lies within the hepatic attachment of the gastro-hepatic omentum (Fig. 325).

Umbilical Veins.—The umbilical vein at birth consists of two parts: (1) A part within the umbilical cord; (2) another within the body, enclosed in the falciform ligament and anterior half of the longitudinal fissure of the

¹ See Scammon and Norris, *Anat. Rec.* 1918, vol. 15, p. 165.

liver. It joins there the ductus venosus and portal sinus (Fig. 325). The arrangement of the umbilical veins in a human embryo of the 3rd week is shown in Fig. 25, and of the 5th week in Fig. 326. The vessel from which the umbilical veins have been evolved—the lateral vein of lower vertebrates—is illustrated in Figs. 27 and 322. In the body stalk the umbilical veins have already fused (Fig. 326), but in the body wall and ventral mesentery, in which they pass to reach the sinus venosus, they remain separate. With the differentiation and closure of the umbilicus, the parts of the body wall in which the umbilical veins are situated are drawn out to form the umbilical cord. The intra-embryonic parts then lie within the ventral mesentery of the fore-gut, lateral and ventral, to the vitelline veins. By the umbilical veins the blood is returned from the placenta to

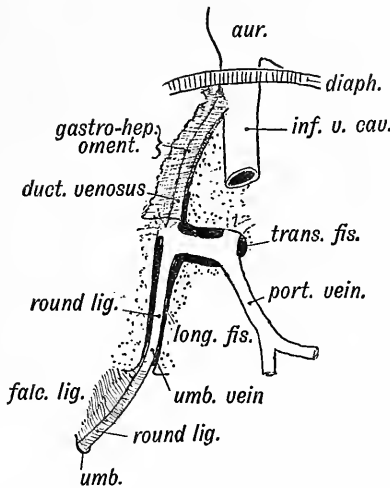


Fig. 325.—Diagram of the Remnants of the Umbilical Vein in the Adult—as seen on the dorso-ventral surface of the liver.

the heart. In nearly all vertebrate embryos the vitelline veins are the first of all the vessels of the body to be developed, but in the Higher Primates, including man, this appears not to be the case. Professor Eternod found that in a human embryo, of about 21 days, the umbilical veins and the venous sinuses of the chorion were already in process of formation, while the vitelline veins had not yet appeared (Fig. 25). We have already seen (Chap. II.) that the Higher Primates are remarkable for the precocious development of the chorion; this early differentiation of the chorion is attended by an equally early formation of the umbilical vessels, which return the blood from the chorion to the heart.

The outgrowth of the liver-bud within the ventral mesentery breaks up not only the vitelline veins, but also the umbilical at their junction with the sinus venosus (Figs. 282, 283). The intra-embryonic part of the **right** umbilical vein atrophies, while the **left** enlarges. With the terminal parts of the vitelline veins the opposite is the case. Thus the umbilical blood as well as the vitelline comes to be poured into the liver. The

termination of the left umbilical vein is gradually transferred during the 6th and 7th weeks from the sinus venosus to the portal sinus (p. 273). The left umbilical vein thus comes into communication with the ductus venosus (see Figs. 324, 325).

The Heart as a Placental Pump.—Having thus traced the origin of the great veins which conduct the blood to the heart we now turn to the development of this organ. In the 4th and 5th weeks the umbilical veins are fully established (Fig. 326) and the heart is receiving the major part of its blood from the chorion, and its chief task is to serve as the

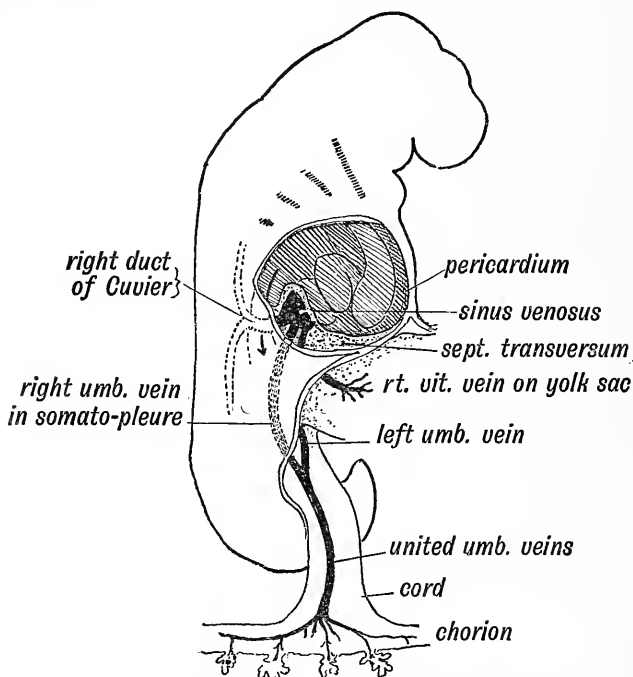


FIG. 326.—Diagram of the Right Umbilical Vein of a 5th week Embryo before the Outgrowth of the Liver Trabeculae. (Modified from His.)

pump of that organ. Hence the large size of the heart and pericardium when compared with the actual dimensions of the embryo itself (Fig. 326)—or the individual organs such as the stomach. Angioblastic cells are being transformed into vascular structures at the end of the 3rd and beginning of the 4th weeks, and although vascularization proceeds at an extremely rapid pace, it is late in the 4th week before an effective circulation has been established.

Cardiac Tubes and Pericardium.—In Fig. 327 is shown a coronal section of the forward projection of the head region of a human embryo in which the neural canal is still open and in which only five body segments are demarcated—about the beginning of the 4th week. The cardiac tubes are seen in process of fusion. Under the fore-gut is seen the angioblastic

cells—representing the endothelial lining of the heart; the walls of the tubes clearly represent foldings of the visceral layer of the mesoderm—for they are seen to be still continuous with the mesodermal covering of the fore-gut. The pericardial part of the coelomic space is already formed. It came into existence during the latter part of the 3rd week—by a process of cleavage which separated the mesoderm lying under the fore-gut into visceral and somatic layers. While the heart tubes are separated from the somatic or parietal layer of mesoderm, they remain attached to the floor of the fore-gut by the **dorsal mesocardium**. No ventral mesocardium is formed. Sections showing the evolutionary origin of the pericardium and of the mesodermal wall of the heart are shown in Figs. 149, 327 and 352.

In Fig. 328 a corresponding section of an embryo a few days older is represented. The process of fusion is complete and already the cardiac

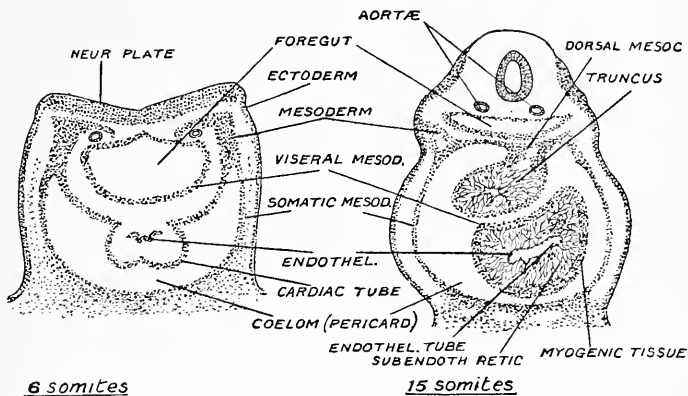


FIG. 327.—Coronal section of Pericardial Region of a Human Embryo with 6 somites—beginning of 4th week. (After Tandler.)

FIG. 328.—Coronal section of Pericardial Region of a Human Embryo with 15 somites—end of 4th week. (After Tandler.)

tube has become elongated and bent so that it is laid open in the section at two places—near where it enters the floor of the fore-gut, to which it is bound by the dorsal mesocardium—and across the segment which will become the ventricles. The angioblastic mesenchyme now forms the endothelial lining of a narrow cardiac lumen; the outer wall—derived from the visceral mesoderm—represents the muscular and epicardial strata, but as yet, although its cells are contractile, they are still in a pre-muscle state. Between endothelial and mesodermal strata is interposed a thick subendothelial reticulum. Into this subendothelial tissue the myogenic cells will proliferate and establish a myocardial sponge-work. The spaces of the reticulum are laden with fluid; there is, then, at this time, under the myocardial wall, a fluid subendothelial cushion.

Arterial and Venous Mesocardia.—The manner in which the tubular cardiac pump is fixed to the wall of the pericardium in a human embryo in the 4th week of development is shown in Fig. 329. The myocardial wall has been stripped off, showing the endothelial lining of the tube. The heart

is fixed at two points only—behind at the place where its first chamber, the sinus venosus, is embedded in the septum transversum—and in front, where its terminal segment, the truncus arteriosus, perforates the roof of the pericardium to enter the wall of the pharynx. At these two points of attachment the epicardial covering of the cardiac tube becomes continuous with the lining membrane of the pericardial cavity; the posterior reflection, on the sinus venosus, is the *venous mesocardium*, the anterior, enclosing the truncus, is the *arterial mesocardium*. The rest of the heart is free within its bursa—the pericardial cavity. For a brief interval there is a dorsal mesocardium, but by the middle of the 4th week only a trace remains on the dorsal wall of the pericardium between the two points of attachment (Fig. 329). At no time is there a ventral mesocardium. The

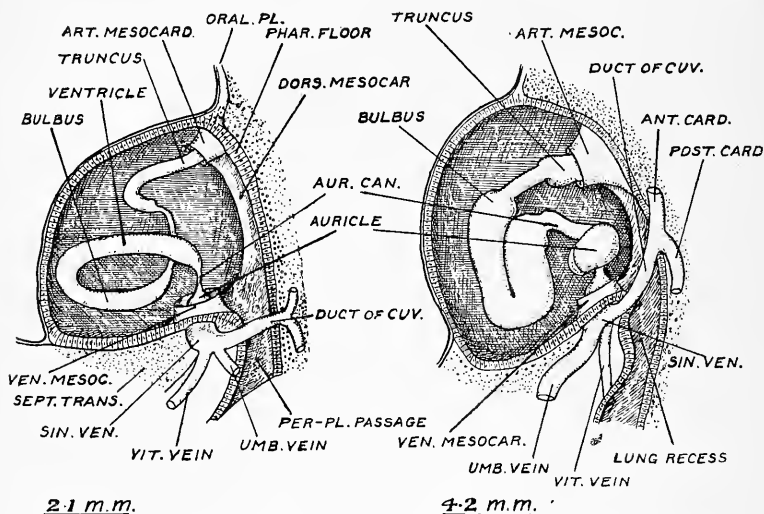


FIG. 329.—The Attachments of the Cardiac Tube—merely its lining membrane is depicted—in a Human Embryo 2.1 mm. long and in the 4th week of development. (After His.)

FIG. 330.—The Attachments of the Heart in a Human Embryo 4.2 mm. long and in the 5th week of development. As in the preceding figure, only the endothelial lining is represented. (After His.)

iter venosum leading from the pericardial to the pleuro-peritoneal cavity is still open; the cardiac tube has grown in length and assumed certain definite bends and twists.

A week later, as shown in Fig. 330, the arterial mesocardium has shifted backwards along the roof of the pericardium and become approximated to the venous mesocardium. There have also been changes in the hinder attachment, for the septum transversum, which is also migrating backwards, has taken up a more oblique position, being now partly on the dorsal wall. The iter venosum, which is reduced in size, is now crossed by the vein or duct of Cuvier, in a slanting direction. By the 3rd month the mesocardia have approximated and the heart has become fixed in its final position (Fig. 354).

Bends, Twists and Primary Chambers.—In the previous paragraph we have seen how the arterial and venous mesocardia become approximated, thus bringing together the ends of the original simple cardiac tube. We are now to see that a similar process takes place in the cardiac tube itself, whereby its auricular (atrial) segment is brought in contact with its terminal or aortic segment. The bends, twists and evaginations of the cardiac tube are easily understood if the reader keeps in mind the manner in which the curvatures of the stomach are produced—namely, by unequal growth. The greater curvature of that organ is due not only to its growth being more rapid than that of the lesser curvature but also to the localized expansion or evagination of the fundus. In some animals there is an actual reduction—an absorption—of the lesser curvature which brings the

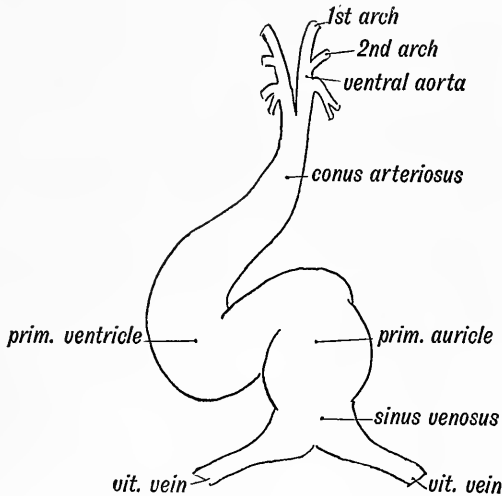


FIG. 331.—The Primitive Divisions of the Embryonic Heart.

pylorus in contact with the oesophagus. The bends, twists and evaginations of the cardiac tube are produced in a similar manner; they are expressions of asymmetrical growth leading up to the stage reached in the fully developed heart.

In Fig. 331 the embryonic heart, early in the 4th week of development, is seen on its ventral aspect and already the primitive ventricular segment of the tube shows a greater curvature towards the right and a sharply bent lesser curvature towards the left. These curvatures are better shown in Figs. 329 and 330; the ends of the primitive ventricular segment are being approximated. The limb of the ventricular loop nearest the beginning of the heart—the proximal limb—will give rise to the 3rd or **ventricular** chamber of the heart; the distal limb will produce the 4th chamber of the heart—the **bulbus cordis**. Besides the ventricular, there is another important curvature at the junction of the auricular with the ventricular segment. The lesser curvature—the sharp angle—of this auriculo-ventricular bend is on the right and ventral aspect of the tube (Fig. 331). The

2nd chamber of the heart—the **auricular or atrial**—is scarcely marked in the early part of the 4th week (Figs. 331, 329), but by the 5th week evaginations are produced on its dorsal side—at the side opposite to the auriculo-ventricular bend (Figs. 330, 332). The **sinus venosus** or 1st chamber of the heart is partly embedded in the septum transversum in the 4th week, while the **truncus arteriosus** or 5th segment of the cardiac tube, which is elongated in the 4th week, is greatly shortened by the 5th (Fig. 329). Further, it will be observed that as early as the 4th week (Fig. 329) there are two constricted segments in the endothelial lining of the cardiac tube—one between the auricular and ventricular segments—the auricular canal, and one between the bulbus and truncus—the bulbar canal. All of these five

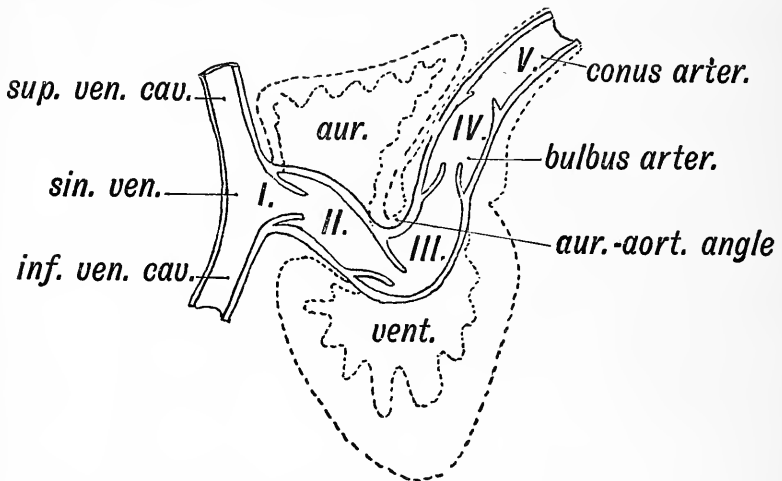


FIG. 332.—Diagram of the five Segments of the Primitive Cardiac Tube. I. The venous segment. II. The auricular segment; on its dorsal aspect the auricle proper is developed; the venous valves are shown between the venous and auricular segments. III. The ventricular segment, the ventricle proper being developed from its ventral aspect. IV. The bulbus segment. V. the truncus, conus or aortic segment. It is separated from the last by the aortic and pulmonary valves.

parts of the cardiac tube are to be seen in the heart of a fish (Fig. 332) such as the shark. The sinus venosus serves as a blood reservoir; the auricle acts as a pump to feed the ventricles, the ventricle is the pump of the gills and body; the bulbus, which becomes incorporated in the right ventricle of the mammalian heart, feeds the gills in diastole, the truncus serves purely as a canal.

The Sinus Venosus.—The sinus venosus, the first chamber of the foetal heart, is formed by the union of the vitelline veins; the umbilical veins and ducts of Cuvier come subsequently to open in it (Fig. 333). The ducts of Cuvier reach it from the somatopleure by passing round the coelomic passages (Figs. 329, 330) and entering the septum transversum. In fish and in the human embryo the sinus serves as a reservoir during systole of the auricle; the systolic wave always commences in the sinus venosus. The right and left **venous valves** (Fig. 335) at the juncture of the

sinus and auricle prevent the regurgitation of blood during systole of the auricle. These valves become more or less atrophied when the right and left sides of the heart are completely separated by the formation of septa.

Fate of the Sinus Venosus (Fig. 334).—Since the sinus venosus plays such a dominant part in the physiology of the heart of lower vertebrates, it is extremely important that we should follow its fate in the human heart. It becomes submerged chiefly in the right auricle, the sulcus terminalis (see Fig. 337), marking the line at which it became included by the upgrowth of auricular tissue. Already, at the end of the 5th week, its orifice has come to occupy a position in the posterior or

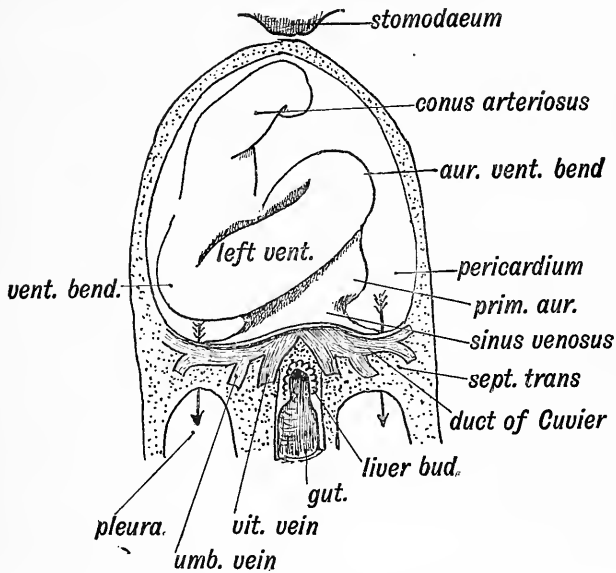


FIG. 333.—Showing the two chief Bends which occur in the Heart during the 4th week.

dorsal wall of the right part of the common auricle (Fig. 335). The part which it forms of the right auricle is indicated by the entrance of the following vessels which primarily terminate in the sinus: (1) The superior vena cava (the right duct of Cuvier); (2) The inferior vena cava, which also opens into the sinus; (3) The oblique vein of Marshall (left duct of Cuvier), which opens into the left horn of the sinus venosus. The left horn of the sinus becomes the coronary sinus. The sulcus terminalis is marked on the interior of the right auricle by a strong muscular band (taenia terminalis), which runs down on the anterior wall of the right auricle from the superior to the inferior vena cava, and indicates the junction of the primitive auricle with the sinus venosus (Fig. 336). The musculature which surrounds the terminal part of the superior vena cava, and that contained in the wall of the coronary sinus, represents the musculature of the sinus. Elsewhere the muscle of the sinus appears to be replaced by that of the auricle.

The Valves of the Sinus Venosus.—Right and left lateral valves (venous valves) guard the entrance of the sinus to the primitive auricle and prevent the regurgitation of blood when the auricle contracts (Fig. 335). The

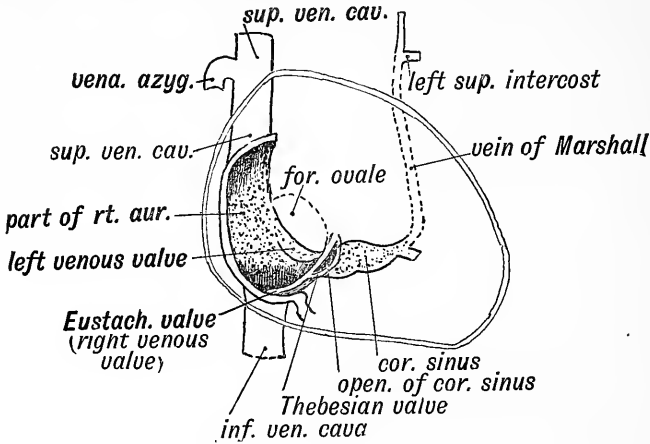


FIG. 334.—Showing the part of the Right Auricle formed from the Sinus Venosus.

valves meet above and form a **superior fornix** in front of the superior caval opening; they meet below in an **inferior fornix**, which, owing to the great shortening of the ventral part of the auricular segment, reaches the base

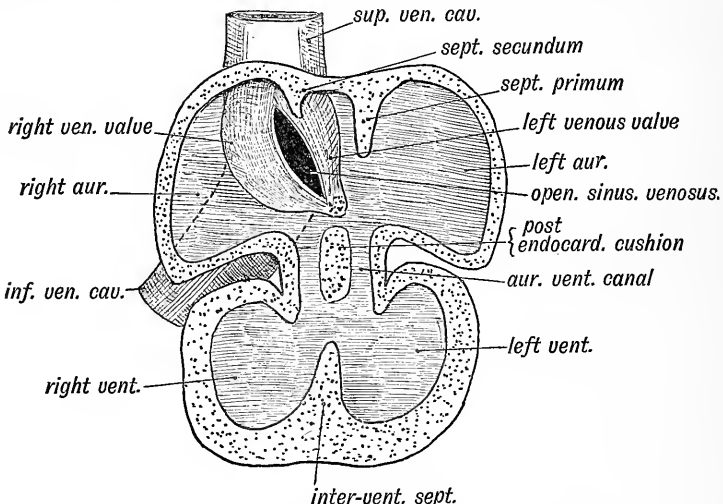


FIG. 335.—Section of the Heart of a 6th week Human Embryo showing the Right and Left Venous Valves which guard the Entrance of the Sinus Venosus into the Primitive Auricle. (After His.)

of the ventricle, and actually fuses with the posterior endocardial cushion (Fig. 342). This has an important bearing on the origin of the auriculo-ventricular (A.V.) bundle within the auricular canal. Along the base of

each valve is arranged a band or taenia of the auricular musculature. Thus each valve consists of a membranous marginal part and a muscular basal part. The right valve in the adult heart becomes (Fig. 336) (1) the Thebesian and (2) Eustachian valves; (3) the musculature at its base forms the taenia terminalis. The left valve becomes (1) a fretted membrane on the septal margin of the inferior caval orifice, (2) a band of musculature accompanying this remnant (Fig. 336).

The Limbic Bands.¹—Two inflections of the wall of the sinus venosus are formed (*a*) between the superior and inferior caval orifices, (*b*) between the inferior caval orifice and that of the coronary sinus. In these inflections

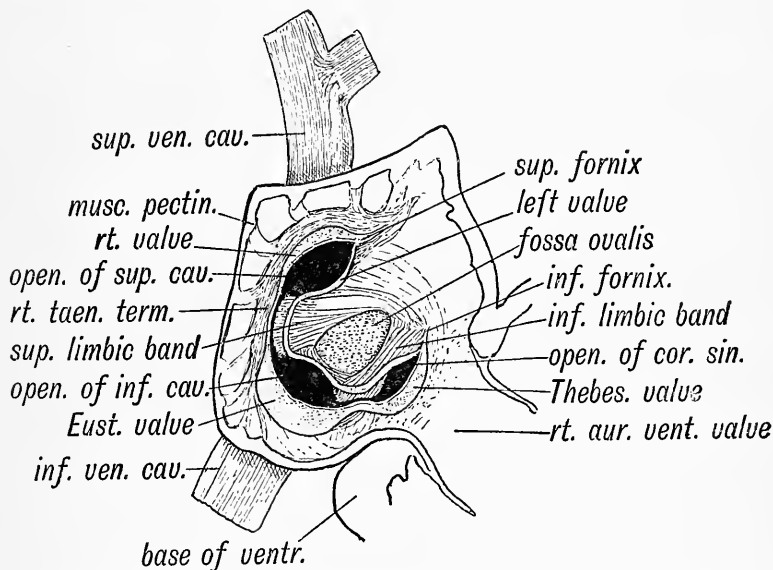


FIG. 336.—Diagram of the Right Auricle thrown open to show the position and relations of the Right and Left Venous Valves and the manner in which they are broken up by the Superior and Inferior Limbic Bands.

bands of auricular musculature cross, forming the upper and lower limbic bands (Fig. 336). Thus the mechanical valves which prevent regurgitation in auricular systole are replaced by a muscular mechanism which serves the same purpose. In amphibians and reptiles, where the division of the heart is incomplete, over-pressure in the right side is relieved by the escape of blood to the left side of the heart; but in birds and mammals such an adjustment is impossible, hence the mechanical venous valves are replaced by a "safety mechanism," which will allow regurgitation from the auricles to the veins if the right side becomes over-distended.

Sino-auricular Node.²—The musculature of the sinus venosus of fishes is made up of small peculiar fibres rich in nuclei and in nerve supply. It

¹ Keith, *Proc. Anat. Soc.* Nov. 1902; *Lancet*, Feb. 27th, March 5th and 12th, 1904; *Journ. Anat. and Physiol.* 1905, vol. 42, p. 1.

² Keith and Flack, *Journ. Anat. and Physiol.* 1907, vol. 41, p. 172; W. Koch, *Verhand. Deutsch. Path. Gesellsch.* 1909, vol. 13, p. 85.

has, more than all the musculature of the heart, the power of automatic rhythmical contraction. In human and mammalian hearts the sinus musculature is replaced by fibres similar to those of the auricle—all but at the sulcus terminalis, which marks the junction of the sinus and auricle. In the sulcus, just in front of the termination of the superior vena cava (Fig. 337), an area of primitive fibres persists—the sino-auricular node. In lower mammals like the mole, the sino-auricular tissue is more extensive; it extends along the greater part of the sulcus terminalis, and passes towards the pulmonary veins. In amphibia and reptiles it extends to the part of the left auricle (vestibule), in which the pulmonary veins terminate. In the lowest mammals—monotremes—the muscular tissue of the node assumes a peculiar form.¹ Thus the higher in the animal scale one ascends, the greater is the reduction of the sino-auricular nodal tissue. It is in reality a neuro-muscular tissue, and is well defined by the 5th month of

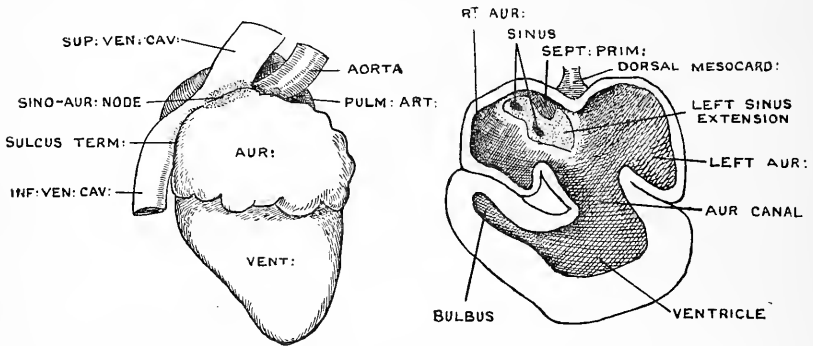


FIG. 337.—Human Heart at the beginning of the 3rd month of development to show the position of the Sino-auricular Node. The unsubmerged strip of sinus venosus is seen between the superior and inferior venae cavae.

FIG. 338.—The Posterior Wall of the Common Auricle of an Embryo of the 5th week, showing the Left Extension of the Sinus Venosus. (His.)

development. Dr. T. Lewis found that the contraction of the heart spread from the sino-auricular node, and gave it the name of the “pace-maker” of the heart.

Formation of the Right Auricle.—The right auricle or atrium is formed by the combination of three parts: (1) the right primitive auricle which appears as a diverticulum from the right dorso-lateral aspect of the auricular segment of the cardiac tube (Fig. 332); it forms the appendix and all that part of the right auricle which is furnished with muscoli pectinati. (2) The auricular canal (Fig. 332) which forms the inner layer of the right auriculo-ventricular valve, and the smooth part of the auricle above the base of that valve. The morphological and physiological junction between the auricle and ventricle is at the lower or free margin of the auriculo-ventricular cusps. (3) The sinus venosus which forms the part of the right auricle between the remnants of the right and left venous valves (Fig. 336).

¹ Dr. Ivy Mackenzie, *Verhand. Deutsch. Path. Gesellsch.* 1910, vol. 14, p. 90.

Formation of the Left Auricle.—The left auricle is also formed by the combination of three parts: (1) the vestibule which arises as an extension round the terminal parts of the pulmonary veins (Figs. 339, 340), (2) the left primitive auricle, and (3) the auricular canal, all of which arise in a manner similar to the corresponding part on the right side. In the human heart the vestibule forms a large part of the left auricle, the primitive auricle being reduced to form merely the appendix (Fig. 340). The vestibule is marked off from the rest of the auricle by a prominent muscular fasciculus—the taenia terminalis sinistra.

Origin of the Vestibule of the Left Auricle.—The representative of the pulmonary veins in fishes—viz. the vein of the swim bladder—ends directly or indirectly in the sinus venosus, a condition which may reappear as an abnormality in the human subject. In the Dipnoi, in which the swim bladder serves as a real lung, the pulmonary vein passes along the

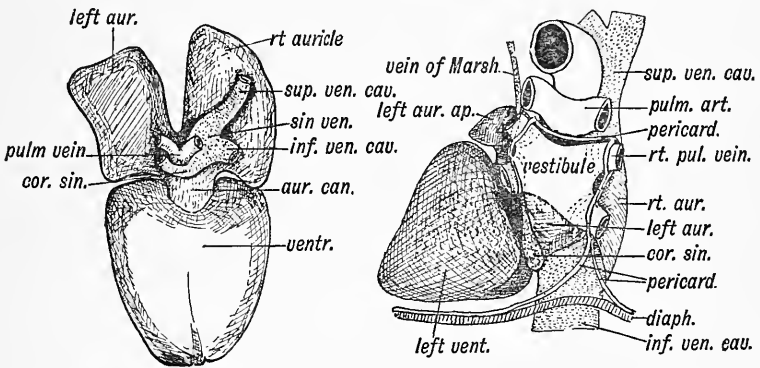


FIG. 339.—Reptilian Heart, viewed on its Dorsal Aspect, to show (1) the manner in which the Auricles arise from the Cardiac Tube, (2) the Auricular Canal, (3) the Sinus Venosus and Great Veins, (4) the Common Pulmonary Vein, which, at its termination, is embraced by the sinus venosus.

FIG. 340.—Heart of Adult viewed from behind to show the Vestibule and the other parts of the Left Auricle. The auricle was in a systolic condition. The remains of the left superior vena cava (vein of Marshall) and the attachment of the pericardium are also indicated.

left wall of the sinus venosus to open in the left auricle near the base of the left venous valve in a manner almost identical to that shown in some abnormal human hearts (see Fig. 371). In the human embryo the pulmonary veins meet in the venous mesocardium, and open by a single orifice as in the Dipnoi. As the lungs develop they grow round and overlap the heart; the right and left pulmonary veins separate; their orifices move apart; later the right and left veins subdivide. With these changes the venous mesocardium is widened, and the part of the auricle in which the veins end is greatly extended to form the vestibule (compare Figs. 339, 340). It is highly probable that the vestibule of the left auricle also represents an extension of the sinus venosus. The late Professor His, who laid our knowledge of the development of the human embryo on a sure foundation of fact—he died in 1904—believed this to be the case. It is certainly so in the heart of amphibians. In Fig. 338 the sinus area will be seen to

extend into the posterior wall of the left auricle. It is on this left extension that the venous channel from the lung buds opens.

Auricular Septa.—During the 6th week the auricular part of the heart becomes separated into right and left chambers by the formation and union of the three following elements: (1) the endocardial cushions, (2) the septum primum, (3) septum secundum. Two **endocardial cushions** arise as thickenings of the endocardium, one on the dorsal or posterior wall, the other on the ventral or anterior wall; they meet and fuse, and thus divide the common auriculo-ventricular canal into the right and left auriculo-ventricular orifices (Fig. 342). In amphibians the endocardial cushions form the dorsal and ventral cusps of the common auriculo-ventricular valve;

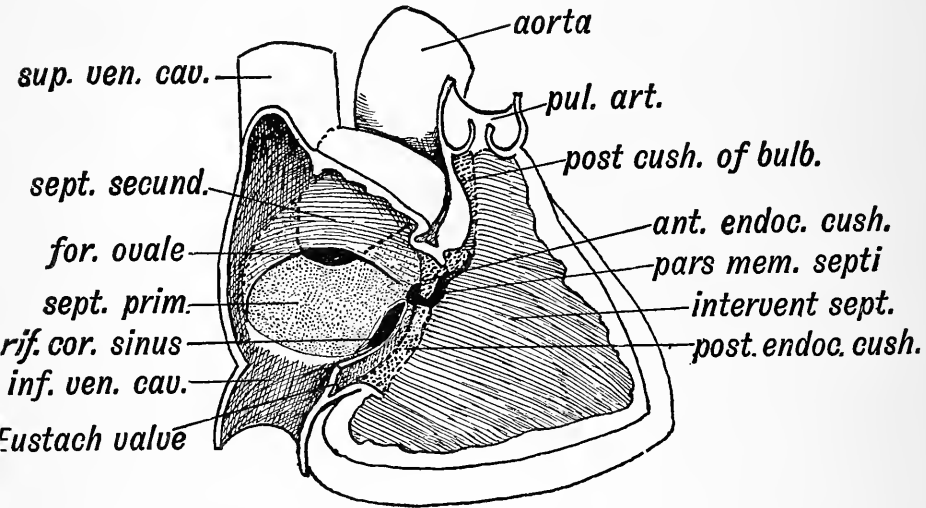


FIG. 341.—Diagram of the opened Right Auricle and Ventricle to show the parts which enter into the Formation of the Septum.

in reptiles these two cusps become united, and thus divide the common auriculo-ventricular orifice into right and left channels; in birds and mammals their fusion is complete. The lower fornix of the venous valves (Figs. 335, 342) becomes implanted on the posterior cushion; thus the sinus comes almost to reach the ventricular chamber. The **septum primum** (Fig. 341) appears at the beginning of the 6th week as a crescentic fold on the roof of the primitive auricle, and while it may actually grow downwards yet appears to be produced mainly by the expansion of the two auricular chambers (Fig. 332). Its lower margin, which is covered by a thickening of endocardial tissue, is attached to both endocardial cushions; the adjacent margins of the septum and endocardial cushions fuse, but occasionally the fusion is incomplete, an inter-auricular foramen (**foramen primum**) being left between the bases of the auriculo-ventricular valves below and septum ovale above (Figs. 341, 348). In mammals and birds the upper part of the septum primum breaks down, the **foramen ovale** being thus formed. The part which remains forms the septum ovale. The **septum**

secundum (Fig. 341) is formed by an inflection of musculature from the roof of the auricle to the right of the septum primum. It forms the annulus ovalis (limbic bands) (Fig. 336) and the musculature of the septum above the foramen ovale (Fig. 336). The foramen ovale thus becomes bounded above by the septum secundum, below by the septum primum. In 25 per cent. of people, according to Fawcett's statistics, the foramen ovale fails to close within the first year after birth, but even when an opening remains blood could pass from the right to the left auricle only when the pressure was greater in the right than in the left. The foramen ovale is an adaptation to the foetal type of respiration; by it the purer blood returning from the placenta can pass from the right to the left side of the heart without passing through the lungs, which are then only partially pervious.

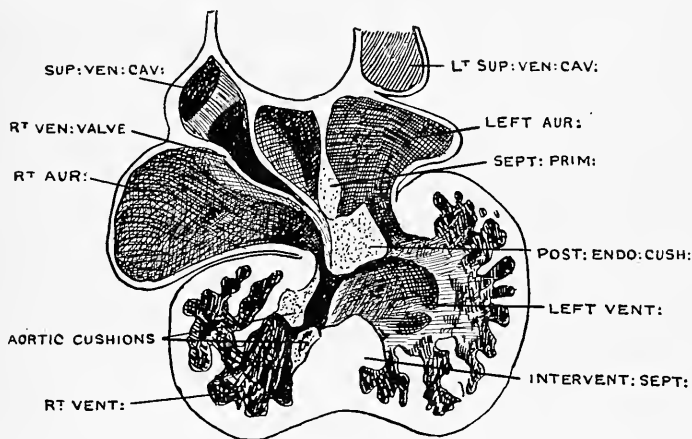


Fig. 342.—Coronal Section of the Heart of a Rabbit, illustrating the condition of parts in the 6th week of Human Development. (Born.)
The cushions labelled "aortic" should be marked "bulbar."

Division of the Truncus Arteriosus.—While the auricular segment of the cardiac tube is undergoing division during the 6th week a similar process is taking place in its terminal segment—the truncus or conus arteriosus, leading to the separation of the pulmonary from the systemic aorta. We have seen that the truncus becomes shortened during the 5th week (Figs. 329, 330) and at the same time the ventral aorta (Fig. 331) is being cleft into right and left vessels. In the 6th week the process of cleavage has reached the origin of the 6th pair of aortic arches from which the pulmonary arteries arise (Fig. 360) so that there now remains but a short segment of the common aortic stem to undergo division and give rise to the intrapericardial part of the aorta and common pulmonary artery. The first step in the division is the appearance of four endocardial cushions at the commencement of the common aortic trunk (Fig. 343, A) the two larger cushions being placed right and left. As is shown in Fig. 343, these cushions become, for the chief part, converted into the aortic and pulmonary valves—but two of them, the right and left, become fused

and assist in forming the spiral septum which separates the aortic from the pulmonary passage. By the end of the 6th week a process of cleavage has

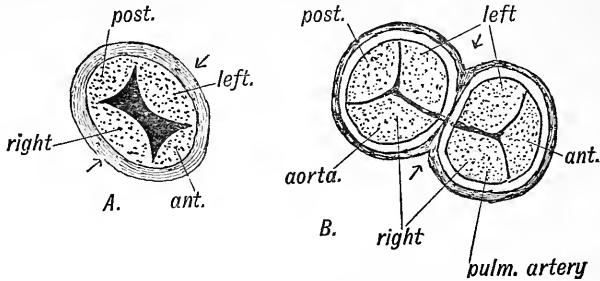


FIG. 343.—The Origin of the Semilunar Valves.

A. The four Endocardial Cushions of the Truncus Arteriosus.

B. The division of the Lateral Cushions to form two Aortic and two Pulmonary Semilunar Valves.

reached the lateral cushions and henceforth the pulmonary artery and aorta form distinct channels.

Bulbus Cordis.¹—We have seen how the first chamber of the heart—the sinus venosus—becomes included in the auricles. In a somewhat

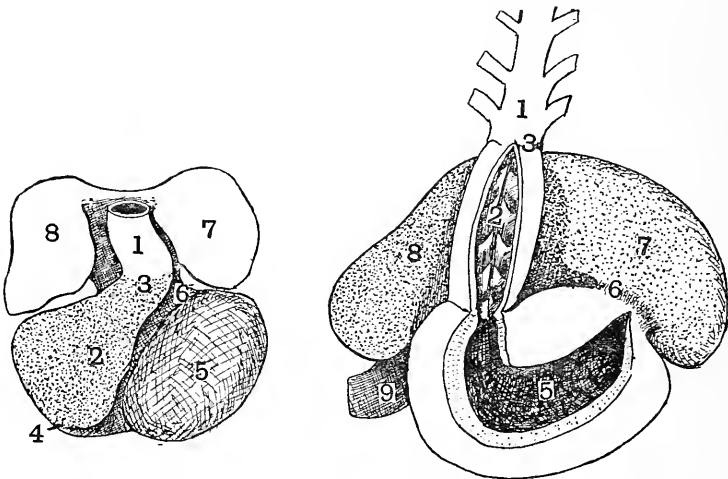


FIG. 344.—Heart of an Embryo of 4 weeks seen from the front. (After His.)
Explanation in text.

FIG. 345.—Heart of a Shark viewed from the front.

similar manner the fourth chamber of the heart—the bulbus cordis—becomes submerged in the ventricles—principally in the right ventricle. In Figs. 344 and 345 the heart of a human embryo and that of a shark are placed side by side. In both the truncus arteriosus (ventral aorta) are

¹ See Greil, *Morph. Jahrb.* 1903, vol. 31, p. 123; Keith, *Lancet*, 1909, Aug. 7, 14, 21; Thompson, *Journ. Anat. and Physiol.* 1907, vol. 42, p. 159; Prof. D. Waterston, *Trans. Roy. Soc. Edin.* 1918, vol. 52, p. 257.

present (1); the bulbus cordis (2); it is lined with valves in the shark and surrounded by cardiac musculature; the bulbus is distinctly marked off from the ventricle at 4, and from the truncus at 3. The ventricle (5) in the shark has the shape of a stomach; in the embryonic human heart a diverticulum or evagination indicating the left ventricle has already appeared (4th week); the auricular canal (6), the left and right auricles (7) (8) are also present. Thus in the human embryo all the parts of the primitive vertebrate heart are represented.

Fate of the Bulbus Cordis.—The fate of the bulbus cordis is most easily understood by a reference to such a diagram as is represented in Fig. 346, *A, B*. The bulbo-ventricular part of the heart in the human embryo resembles the stomach; there is a greater and a lesser curvature. In the second month the lesser curvature, represented in the diagram by a heavy black line, undergoes a process of atrophy. The result is (Fig.

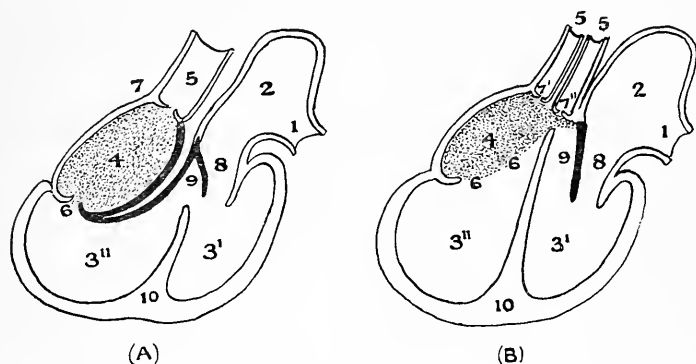


FIG. 346, *A*.—Diagrammatic Section of the Embryonic Heart in the 3rd week.

B.—Diagrammatic Section of the Foetal Heart at the 3rd month.

1, sinus venosus; 2, auricle; 3', 3'', left and right ventricles; 4, bulbus cordis; 5, common aorta; 6, auricular canal; 7, 8, auricles; 9, bulbo-ventricular junction; 10, truncus arteriosus.

346, *B*) that the cavity of the bulbus becomes thrown into that of the ventricle and the auriculo-ventricular and aortic orifices are brought side by side. At this time, when the lesser curvature is disappearing, the cavities of the ventricles are appearing by an evagination or enlargement of the ventricular wall, leaving the interventricular septum between the evaginations (Figs. 288, 298). The conus or truncus arteriosus is dividing then into systemic and pulmonary aortae. Thus it comes about that the cavity of the bulbus cordis is converted into the infundibulum of the right ventricle, merely a trace extending across to the left ventricle above the interventricular septum. The importance of recognizing the bulbus cordis as a separate constituent of the heart will be realized when it is remembered that 95 per cent. of the cases of congenital malformation are the result of its imperfect transformation to form the infundibulum of the right ventricle of the heart. In nearly every case of what is described as **congenital stenosis** of the pulmonary orifice, a cavity of variable size will be found under the malformed valves representing the bulbus cordis. In fishes the

bulbus is connected with the blood supply to the gills; its derivative, the infundibulum of the right ventricle, has to do with the regulation of the blood supply to the lungs, but in neither case do we know the exact function of this part of the heart.

Bulbar Cushions.¹—During the transformation of the bulbus in the 6th week, there appear within it two endocardial cushions—evolved from the series of valves which line the bulbus of the primitive heart (Fig. 345). The part taken by them in building up the interventricular septum can best be realized when the infundibular part of the right ventricle is exposed as in Fig. 341. The line of fusion between the posterior and anterior bulbar cushions is seen to descend in the septal wall of the infundibulum from the pulmonary valves to the site of the interventricular foramen. When the bulbar cushions fuse at the end of the 6th week the small sub-

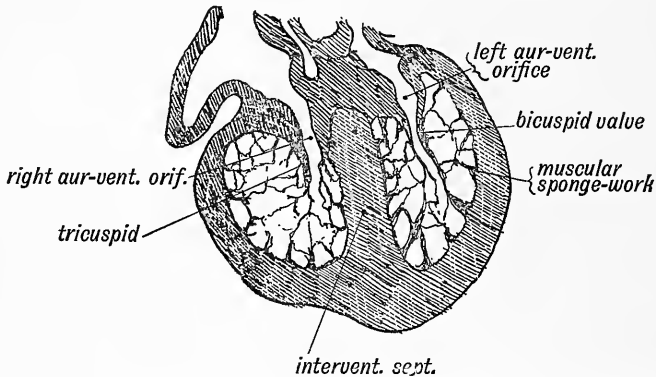


FIG. 347.—Section of the Ventricles of the Foetal Heart, showing the Muscular Sponge-work within their Cavities. (After His.)

aortic part of the bulbus becomes separated from the main part included in the infundibulum of the right ventricle (Figs. 346, *A*, *B*). The bulbar cushions at an early stage of development are shown in Fig. 342, where they are wrongly labelled aortic cushions.

Formation of the Ventricles.—Along the lateral and convex aspects of the ventricular tube the musculature grows rapidly, forming a dense superficial layer and a deep sponge-work system of trabeculae, which almost fill the ventricular chamber. In the hearts of fishes and amphibians the sponge-work persists, but in birds and mammals the ventricular chambers are formed as diverticula by the absorption of the sponge-work. Between the right and left excavations, however, part of the sponge-work is left to form the interventricular septum (Fig. 347). In front the musculature of the septum is attached to the anterior cushion of the bulbus arteriosus (Figs. 341, 342); behind, it is attached to the posterior of the two endocardial cushions in the auricular canal. On its upper free crescentic margin is a thickening of endocardial tissue. The closure of the **interventricular foramen** completes the separation of the left from the

¹ For full details regarding the formation of the interventricular septa, see Prof. Frazer's research, *Journ. Anat.* 1917, vol. 51, p. 19.

right ventricle of the heart. It is bounded below by the margin of the interventricular septum; above, by the bulbar cushions and behind by the auricular endocardial cushions (Figs. 341, 350). The **pars membranacea septi**, which is found beneath the base of the septal cusp of the tricuspid, and below the septal cusps of the aortic valve, is formed towards the end of the 7th week, by the fusion of the endocardial margins of the interventricular foramen.¹ The foramen is thus closed by that process to which the name of zygosis has been given (p. 287). Only in mammals and birds is the interventricular foramen closed, the foramen ovale opened and the venous valves replaced by a muscular mechanism.

Abnormalities of the Heart.²—Thus five elements enter into the formation of the septum of the heart, the two interauricular septa, the two endocardial cushions of the auricular canal, the interventricular septum, the endocardial cushions of the bulbus and the cushions of the truncus

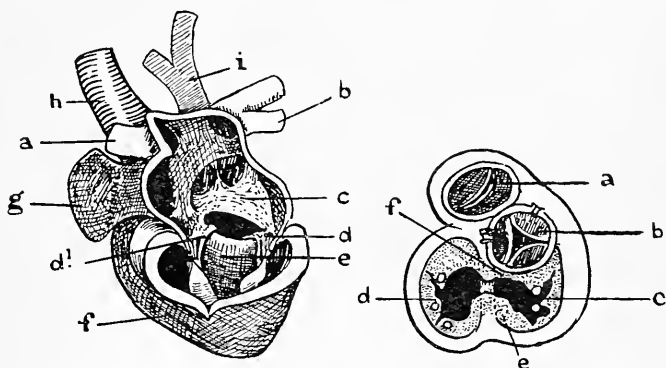


FIG. 348.—Abnormal Heart of a Child with the Left Auricle and Ventricle laid open. *a*, left; *b*, right pulmonary veins; *c*, septum primum; *d*, *d'*, posterior and anterior endocardial cushions; *e*, interventricular septum; *f*, left ventricle; *g*, left auricular appendix; *h*, aorta; *i*, sup. vena cava.

FIG. 349.—Same Heart from above. *a*, the orifice of pulmonary artery with fusion of septal cusps; *b*, valves of aorta, with the coronary arteries rising above septal cusps; *c*, *d*, *e*, *f*, continuity of the tricuspid and mitral valves across the upper border of septum.

arteriosus (Fig. 341). Abnormalities may result from their non-union, but by far the commonest defect found is a patency of the interventricular foramen (Fig. 350). This is accompanied in nearly every case by an arrest in the expansion of the bulbus cordis and a stenosis or narrowing at the orifice of the pulmonary artery (**congenital pulmonary stenosis**). The blood of the right ventricle, in such cases, is pumped into the aorta, through the interventricular foramen; blood is supplied to the lungs through the ductus arteriosus or by the bronchial arteries from the aorta.

Auriculo-Ventricular Valves.—At first the auricular canal is exposed on the surface of the heart (Fig. 294), but it soon becomes enveloped

¹ For a fuller account of development of ventricles see F. P. Mall, *Amer. Journ. Anat.* 1912, vol. 13, p. 249; Frazer, *Journ. Anat.* 1917, vol. 51, p. 19.

² A. Keith, *Journ. Anat. and Physiol.* 1912, vol. 46, p. 211; F. T. Lewis and Maude Abbott, *Bulletin Med. Museums*, 1916, vol. 6, p. 1.

by the upgrowth and excavation of the bases of the ventricles (Fig. 338). The auricular canal, with an attenuated envelopment derived from the ventricle, thus comes to hang within the ventricular chambers and forms the lateral cusps of the tricuspid and mitral valve (Fig. 347). The septal cusps are formed from processes of the endocardial cushions (Fig. 349). The chordae tendineae, musculari papillares, columnae carneaе, trabeculae and moderator band are derived from the muscular sponge-work of the ventricles.

Various maldevelopments of the heart throw light on the nature of the auriculo-ventricular valves. In Fig. 348 an abnormality of this kind is represented. The anterior and posterior endocardial cushions have not united, hence the tricuspid and mitral valves are continuous across the upper border of the septum (Fig. 349). The aperture seen above the interventricular septum is the *foramen primum*—not the interventricular foramen.

CHAPTER XXI.

CIRCULATORY SYSTEM (*Continued*).

Purkinje System of the Heart.—About the middle of the nineteenth century, Purkinje, Professor of Anatomy at Breslau, discovered large peculiar muscle fibres beneath the endocardium of the heart of the sheep and of other ungulate animals. In 1906 Tawara showed that such fibres were connected with a muscular bundle, which rose in the wall of the auricle near the orifice of the coronary sinus and entered the ventricle along the upper border of the interventricular system.¹ In many cases of malformed heart the primitive relations of the **auriculo-ventricular (A.V.)**

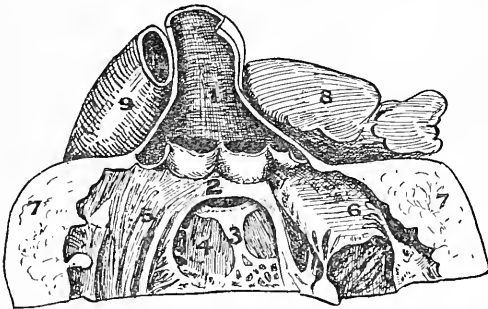


FIG. 350.—The Auriculo-ventricular Bundle in a Heart with open Interventricular Foramen. 1, aorta; 2, on the site of the pars membranacea septi; 3, left division issuing from bundle situated on the upper margin of the interventricular septum (4); 5, anterior wall of left ventricle; 6, mitral valve; 7, cut wall of left ventricle; 8, left auricle; 9, pulmonary artery.

bundle may be seen (Fig. 350). It passes along the upper border of the interventricular septum below the interventricular foramen. Its left branch descends on the septum to the musculari papillares of the left ventricle; the right division or branch passes along the moderator band, which marks the junction of the bulbus cordis with the body of the right ventricle. When it is remembered that the ventricles arise from evaginations of the ventricular tube, it will be seen that the bundle on the upper border of the septum occupies the least disturbed part of the lumen of the primitive cardiac tube.

The evolution of the Purkinje system may be realized from a study of Fig. 351. Gaskell found in 1883 that the auricles and ventricles were

¹ For an account of Tawara's discovery see Keith, *Lancet*, 1906, Aug. 11.

connected in fishes, amphibians and reptiles by the musculature of the auricular canal (Fig. 351, 4, 4), and that this connection conveyed the wave of contraction from auricle to ventricle. The auriculo-ventricular muscular collar begins in a ring of peculiar muscle cells situated as shown in Fig. 351, 3, 3. In the mammalian heart the primitive muscle of the auriculo-ventricular canal disappears—except at the upper border of the septum, where it forms the bundle. The node in which it arises represents a remnant of the ring of peculiar muscular tissue which surrounds the auriculo-ventricular junction. It is true that the sinus venosus reaches the posterior endocardial cushions (Fig. 342) near the site of the node, but it is most

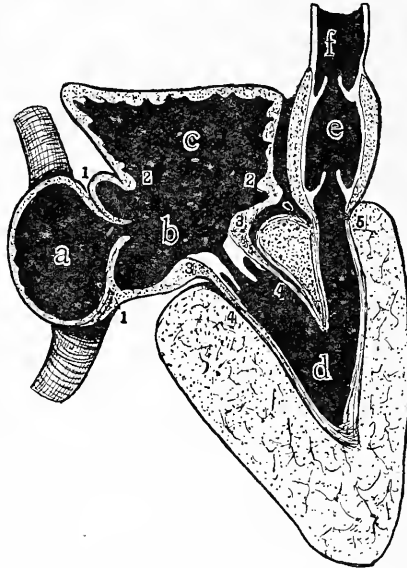


FIG. 351.—Section of a Generalized Type of Heart to show the Origin of the Auriculo-ventricular Bundle and Node. *a*, sinus venosus; *b*, auricular canal; *c*, auricle; *d*, ventricle; *e*, bulbus cordis; *f*, aorta; 1, 1, sino-auricular junction; 2, 2, auricular junction with canal; 3, 3, auricular ring of peculiar fibres; 4, 4, auriculo-ventricular musculature; 5, 5, bulbo-ventricular junction.

improbable, in the light of comparative anatomy, that the node at the commencement of the bundle should represent sinus musculature.

Changes in the Circulation at Birth.—(1) The outflow of the blood to the placenta by the hypogastric arteries and its return by the umbilical vein is arrested when the umbilical cord is tied.¹ The umbilical vein and ductus venosus gradually become ligamentous. (2) The first breath expands not only the air spaces of the lungs, but also the pulmonary vessels, so that the pressure within them becomes less than in the aorta; hence the blood in the pulmonary aorta passes through the lungs instead of gaining the aorta by the ductus arteriosus. A section across the ductus arteriosus and aorta (Fig. 353) shows that, before birth, the septal wall of the ductus is invaginated within the lumen of the aorta; after birth the

¹ For changes in vessels see A. W. Meyer, *Amer. Journ. Anat.* 1914, vol. 16, p. 477.

septal wall is bent within the lumen of the ductus, thus partly closing it. (3) The foramen ovale is closed by the pressure within the left auricle being raised by the inflow of pulmonary blood, the pressure in the left auricle then reaching a higher point than in the right auricle. The closure of the foramen is assisted by an alteration in the action of the limbic bands (Fig. 336) brought about by their indirect attachment to the diaphragm. (4) The hypogastric arteries, beyond the origin of the vesical arteries, become reduced to cords. (5) The pressure within the aorta becomes three times that in the pulmonary arteries; the left ventricular wall becomes three times as thick as that of the right. Before birth the ventricular pressures were equal and so were the thicknesses of the ventricular walls.

Remnants of the Foetal Circulation in the Adult.—The nature of these remnants has been already described; they need be only enumerated here. They are:

(1) The Obliterated Hypogastric Arteries; (2) The Umbilicus; (3) The Round Ligament of the Liver; (4) The Fibrous Remnant of the Ductus Venosus; (5) The Eustachian Valve; (6) The Foramen Ovale; (7) The Fibrous Remnant of the Ductus Arteriosus.

Changes in the Position of the Heart.—The alteration in the position of the heart from a subpharyngeal to a thoracic position during the 5th, 6th and 7th weeks of development is brought about by two factors. First, the heart is primarily a pump for forcing the blood through the organ of

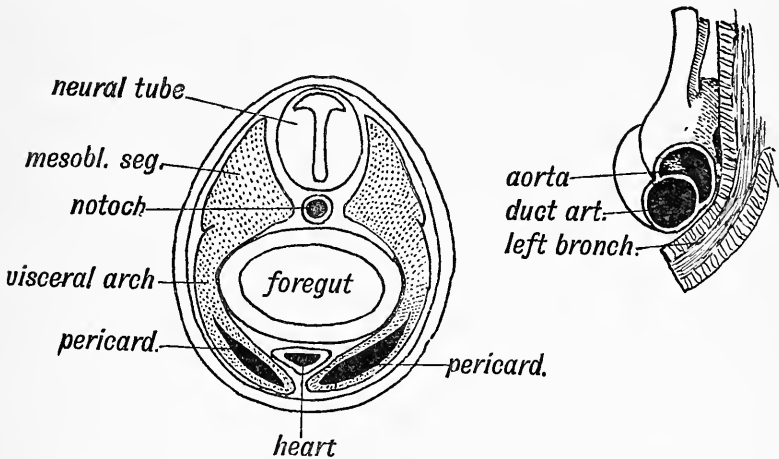


FIG. 352.—Diagrammatic Section across the Head Fold of a developing Salamander to show the relationship of the Pericardial part of the Coelom to the Heart and Fore-gut. (After C. Rabl.)

FIG. 353.—Section across the Junction of the Aorta and Ductus Arteriosus (viewed from behind) of a full time Foetus to show the Inflection of the Wall of the Ductus within the Lumen of the Aorta.

respiration; hence in the fish it lies beneath the gills, in air-breathing vertebrates it is situated close to the roots of the lungs. Secondly, in reptiles, birds and mammals a neck is developed, the head and pharyngeal region being gradually forced forwards, while the heart and pericardium

come to lie opposite the middle part of the dorsal region of the spine. The neck is differentiated in the human foetus during the second month. All the structures in the neck become elongated—the oesophagus, trachea, vagus nerves, jugular veins and carotid arteries. During this change the arch of the aorta and its branches are evolved from the ventral stems of the aortae and aortic arches. In most mammals the *left carotid* arises in common with the aortic stem, and a reversion to this type is the commonest abnormality to which the aortic arch is liable in man (Parsons). The separation of the left carotid from the innominate in man is due to the large size of the upper aperture of his thorax. The left vertebral artery or the thyroidea ima may gain an origin from the aortic arch.

Final Fixation of Heart.—As may be seen from Figs. 329 and 355, the heart of the human embryo is fixed within the pericardium exactly as in a

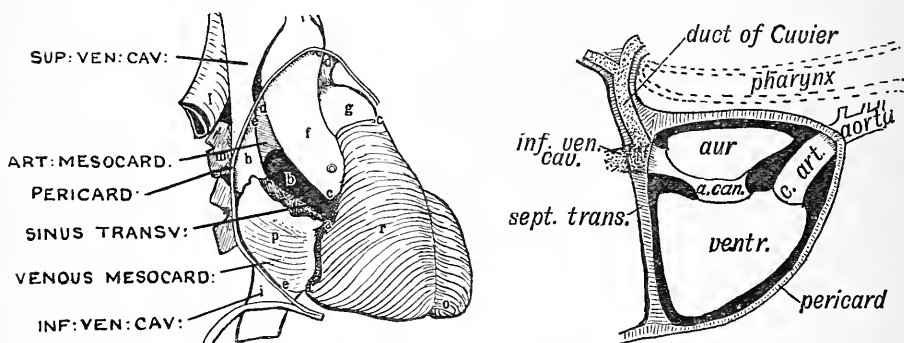


FIG. 354.—The Heart pulled forwards to show its two Attachments by the Arterial (*d, d*) and Venous (*e, e*) Mesocardia.

FIG. 355.—Diagram of the Heart of a Fish to show: (1) the Primitive Parts of the Heart; (2) the Relationship of the Heart to the Pharynx; (3) the Septum Transversum; (4) the fixation of the Heart.

fish—being attached behind to the septum transversum by the venous mesocardium and under the pharynx, by the arterial mesocardium. By the 8th week the interventricular septum is complete and the heart has taken up its position in the thorax, being fixed within the pericardium in the same manner as in the adult (Fig. 354). The original mesocardia can still be recognized, separated by the transverse sinus of the pericardium (Fig. 354, *b*). The sinus is also shown in Fig. 356. The derivatives of the truncus arteriosus—the aortic root and pulmonary arteries—lie within the reflections of the arterial mesocardium; the caval and pulmonary veins reach the auricles through the reflections of the venous mesocardium. That part of the septum transversum which contained the sinus venosus and great veins has become an intrinsic part of the dorsal wall of the pericardium. The heart has so doubled on itself that the venous and arterial mesocardia are in contact, being only separated by a *potential* space—the transverse sinus (Fig. 356).

The venous mesocardium becomes much more extensive by the ingrowth and separation of the pulmonary veins. These grow in from the lungs, and pierce the pericardium to reach the left auricle (Fig. 356). They

reach the auricle through the mesentery or venous mesocardium of the sinus venosus. The migration of the left pulmonary veins causes a prolongation of the venous mesocardium to the left side; when the heart is removed the venous mesocardium is seen to be F-shaped in section. The oblique sinus lies in the concavity of the pulmonary venous mesocardium (Fig. 356).

Primitive Relationships of the Pericardium.—Were one to restore the head and pericardium to the relative positions they occupy in the 5th week of development, then the pericardium must be lifted from the thorax and placed beneath the chin and larynx so that the septum transversum is opposite the origin of the phrenic nerve from the 4th cervical segment; the anterior border of the umbilicus is also then opposite the origin of the phrenic nerve. In the somatopleure over the pericardium and between

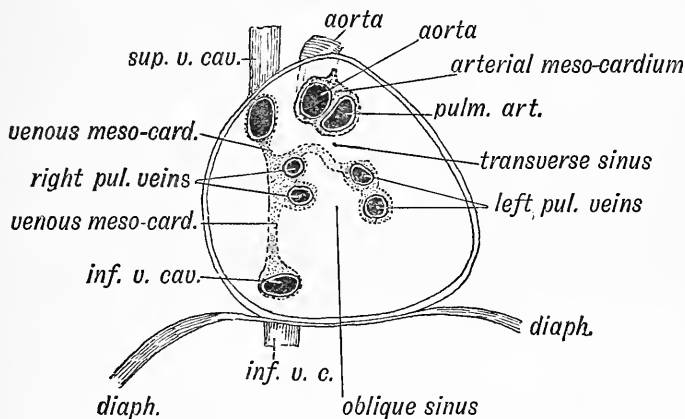


FIG. 356.—View of the Interior of the Pericardium showing the Attachments of the Heart to its Dorsal Aspect by the Arterial or Venous Mesocardia.

the mandible and umbilicus are developed the depressors of the hyoid, the sternum and sternal ribs. The pericardium is therefore the coelom of the neck; its fibrous wall represents the deepest layer of the cervical somatopleure, corresponding to the fascia transversalis of the abdomen. With the elongation of the neck and separation of the pharynx and pericardium, the tissue of the branchial segments which surrounds the aortic arches is drawn out to form the carotid sheaths.

Ectopia Cordis.—Occasionally children are born with their hearts exposed on the surface of the chest. In extreme cases only the dorsal wall of the pericardium is present, and it is flush and continuous with the skin of the chest. In these cases the sternum is partially absent, or if present it is cleft, the right and left halves being widely parted. No satisfactory embryological explanation of this condition has yet been given.

Dorsal Aortae.—The dorsal or descending aorta, like the heart, is bilateral in origin. At the beginning of the 4th week, as somites are being demar-

cated in the cervical region of the embryonic plate, the right and left dorsal aortae, commencing at the upper ends of the pharyngeal arches, pass backwards side by side, supplying branches to the archenteron as they go (Fig. 25). From their terminal branches on the yolk sac commence the umbilical arteries (Fig. 25). By the end of the 4th week the dorsal aortae have fused to form one vessel from the 1st thoracic to the 1st lumbar segment. At this date the radicles of the **umbilical arteries** arise from the aorta opposite the 1st lumbar segment; by the end of the 5th week their origin has migrated backwards to the level of the last lumbar segment. Although the umbilical arteries appear to be direct continuations of the dorsal aortae in later embryonic and foetal life, yet there can be no doubt that this honour falls to the middle sacral artery, for, as we have seen (p. 27), the umbilical arteries must be regarded as greatly modified vesical or allantoic branches of the aorta. The middle sacral artery is formed by the fusion of the caudal arteries—morphological continuations of the dorsal aortae. The coeliac axis,¹ superior and inferior mesenteric arteries are the sole survivors of the numerous branches supplied by the paired aortae to the archenteron. At the end of the 5th week the **coeliac axis** arises from the aorta opposite the 7th cervical segment; by the end of the 7th week its origin is opposite the 10th thoracic segment—its permanent position. The superior and inferior mesenteric arteries undergo a corresponding degree of migration backwards during the 6th and 7th weeks.

Formation of Blood Vessels.²—The development of blood vessels and blood corpuscles can best be studied in the mesoderm which covers the yolk sac, for in the human embryo, with the exception of the chorion, the wall of the yolk sac is the site at which vessels and blood are first formed. The mesodermal cells covering the yolk sac show a differentiation into two strata—a superficial or **mesothelial**, representing the peritoneum and a deeper or **mesenchymal**, lying between the mesothelium and the entodermal lining of the sac (Fig. 357). The cells of the mesenchyme, as already mentioned (p. 40), are angioblastic or vaso-formative in nature. Originally their cell-bodies are continuous and form a syncytium, but in Fig. 357, *A* this continuity is disappearing and a mass of mesenchymal cells is being separated to lie within a blood space. In the wall of the space certain cells are being differentiated to form a lining membrane. The blood space, the cells within it and the enclosing endothelium constitute a **blood island**. In the island are to be seen certain mesenchymal cells—**haemoblasts**—which represent the parent type of all blood cells—both white and red. In the same island (Fig. 357, *A*) are to be seen certain haemoblasts in which haemoglobin is being formed, thus becoming erythroblasts—the parent type of red cells. They represent cells which are being set aside as oxygen-

¹ Broman, *Anat. Hefte*, 1908, vol. 36, p. 405.

² For recent literature on origin of blood and vessels: see H. E. Jordan, *Amer. Journ. Anat.* 1916, vol. 19, p. 227; C. R. Stockard, *ibid.* 1915, vol. 18, pp. 227, 525; R. D. Lillie, *ibid.* 1919, vol. 26, p. 209; Vera Danckhoff, *ibid.* 1918, vol. 24, p. 1, *Anat. Rec.* 1916, vol. 10, p. 415; Florence Sabin, *Contributions to Embryology*, 1917, vol. 6, p. 61; 1920, vol. 9, p. 213.

carriers and are therefore to be counted units of the respiratory system. Further, in such an island (Fig. 357, *A*) are to be recognized large lymphocytes—or leucoblasts—the parent type of white corpuscles.

The blood islands scattered over the yolk sac become confluent by the union and canaliculization of intervening endothelial cells. In this manner a vascular network is produced on the yolk sac; the manner in which the blood islands are united is typical of the manner in which new blood channels are formed. Within the body of the embryo mesenchymal cells assemble in vasoformative groups, become canaliculized and unite with neighbouring groups to form both arteries and veins. The endothelial cells of capillaries retain throughout life the vasoformative power which characterizes them during the period of development and growth. The cellular processes at the growing point of a capillary are permeable at first

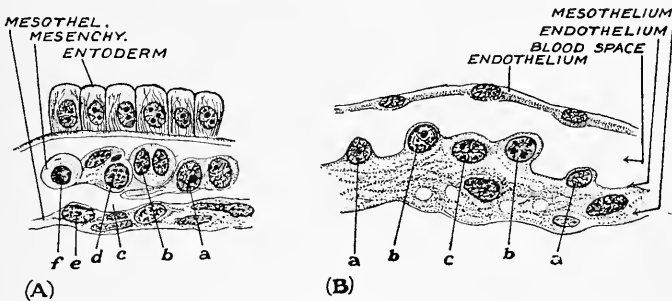


FIG. 357.—*A*, Section of the Wall of the Yolk Sac to show the constitution of a Blood Island. (H. E. Jordan.)

a, Haemoblast, dividing; *b*, Erythroblast, dividing; *c*, Blood-space; *d*, Haemoblast; *e*, Endothelial cell; *f*, Leucoblast.

B, Wall of a Blood-space, showing Blood Cells arising from its Endothelium. (H. E. Jordan.)

a, Endothelial Cell; *b*, Haemoblast being produced from Endothelial Cell; *c*, Haemoblast arising outside Blood-space from Endothelium.

to the plasma only, subsequently the lumen becomes large enough to allow the blood cells to pass.

Formation of Blood.—In the development of each system of the human body the various parts appear in the same order as they are seen to occur in ascending the scale of the animal kingdom. In many invertebrates the blood is formed by only a fluid living intercellular substance—the **plasma**; when the human heart beats first, its lumen contains no blood cells, only plasma. In amphioxus nucleated uncoloured corpuscles appear in the plasma; the cells which appear first (during the 4th week) in the circulation of the human embryo are the red nucleated corpuscles (erythroblasts) formed in blood islands. In all vertebrates, with the exception of amphioxus, nucleated white as well as nucleated red cells appear in the blood; in the human embryo the white cells (leucocytes) appear somewhat later than the red. In mammals only do the nuclei disappear or become extruded from the erythroblasts, red blood corpuscles (erythroplastids) being thus formed. The erythroplastids begin to appear in the blood of the human embryo before the end of the 2nd month, and

gradually replace the erythroblasts, which cease to appear in the circulating blood some days after birth (Ham). At every period erythroblasts are formed as derivatives of the endothelium of vascular walls. The mode in which blood cells arise from the endothelial lining of blood spaces is illustrated in Fig. 357, *B*.

The Germinal Centres for Red Blood Corpuscles.—At every period of life the red blood corpuscles (erythroplastids) arise from erythroblasts. These are formed first in the blood islands of the chorion, of the yolk sac and within vascular extensions of the vasoformative cells throughout the body. The formation of blood corpuscles in the liver commences at the beginning of the second month of development, and ceases in the later months of foetal life.¹ The parent erythroblasts lie side by side with the liver cells. The splenic blood spaces are also sites of blood formation in

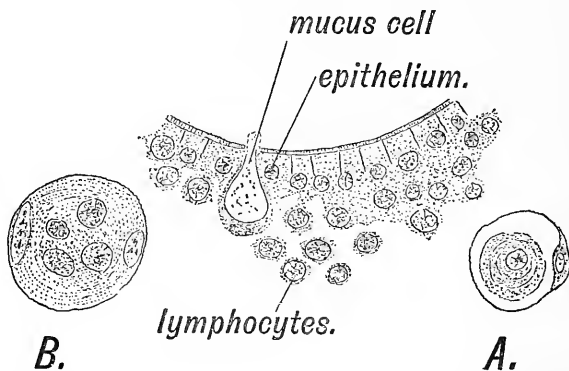


FIG. 358.—Section of a tubular part of the Thymus of a Frog, showing (1) the Production of Lymphocytes from the Thymic Epithelium; (2) the Production of Hassall's Corpuscles. In *A* a leucocyte within the wall of a capillary has become enlarged and shows concentric striae; in *B* the nucleus of the leucocytes has undergone division; it completely fills the lumen of the capillary, the nuclei of which are seen in the periphery of the body. (After Nusbrum and Machowski.)

the latter half of foetal life. About the middle of foetal life the capillaries of bone marrow begin to be invaded by angioblastic outgrowths, and from birth onwards the capillaries of the red bone marrow become the breeding ground of erythroblasts, from which the red corpuscles arise by disappearance of their nuclei.

Origin of White Blood Corpuscles.²—The reticular tissue which underlies the epithelial lining of the alimentary tract corresponds to the mesenchymal angioblastic stratum of the yolk sac and, from the 5th month of foetal life onwards, is the seat of a prolific production of lymphocytes. The apparent production of lymphocytes direct from entodermal cells (Fig. 358), such as are represented in the tonsillar and thymic outgrowths, is probably due to the fact that such outgrowths always are in the closest apposition to this lymphocyte-producing mesenchymal stratum.

¹ See Mollier, *Archiv. für Mikroskopische Anat.* 1909, Bd. 74, p. 474.

² See Retterer et Lelievre, *Journ. d'Anat. et Physiol.* 1912, vol. 48, pp. 14, 194; F. Weidenreich, *Ergebnisse der Anat.* 1909, vol. 19, p. 527. See also references on p. 261.

Leucocytes are also profusely produced from (1) the endothelium of serous cavities—such as the peritoneum and pleura; (2) from the endothelium of lymphatic vessels; (3) from leucoblasts of bone marrow; (4) from the endothelium of capillaries, and possibly (5) from connective tissue cells. As yet, however, these statements must be accepted with reserve, for there is still a degree of uncertainty regarding the genetic relationship of one form of leucocyte to other forms. Mollier, who has recently studied the development of the blood corpuscles, describes the liver as the chief source of white blood corpuscles during foetal life; later the site of their formation is shifted to the blood spaces in marrow. He regards both basophile and eosinophile leucocytes as arising in the liver from the same parent cells (haematoblasts) as give origin to the red nucleated corpuscles.

Lymphatic System.—In all vertebrate animals the plasma or lymph from the tissues of the body is drained into the veins by a special system—the lymphatic vessels. In amphibia the lymph collects in large spaces lined by endothelium, from which it is forced into the venous system by two pairs of lymph hearts—one pair situated in the angle between the jugular and subclavian veins, the other pair between the internal and external iliac veins. In mammals the lymph hearts disappear; they are no longer required, for the negative pressure in the veins of the thorax, set up by the evolution of a separate respiratory cavity, is sufficient to draw the lymph into the venous system. It is remarkable, however, that Miss Sabin who, by a paper¹ published in 1902, inaugurated our knowledge of the development of the mammalian lymphatic system, found that the lymph vessels appear first at those four points where the amphibian lymph hearts are situated.

Recent enquiries by American embryologists have thrown quite a new light on the origin of the lymphatic system. They have established that the formation of lymph vessels begins at definite centres and from such a centre vessels spread outwards, vascularize and drain a definite area. If the starting centre is excised, then there is no outgrowth and vessels from neighbouring areas invade and drain the one thus deprived. While the angioblasts of the blood system are everywhere and have established a complete vascularization of the embryonic tissues before the end of the 4th week, the angioblasts of the lymphatic system do not become manifest until the end of the 6th week, when they form a capillary network in the centres of initiation. The greatest and earliest centre is situated in the angle between the jugular and subclavian veins, where the termination of the thoracic duct is afterwards formed. By the end of the 8th week

¹ Florence R. Sabin, *American Journ. of Anat.* vol. 1, 1902, p. 367. In nearly every subsequent volume will be found some of the important contributions made to our knowledge of the development of lymphatics by modern American embryologists. F. T. Lewis, *Amer. Journ. Anat.* 1909, vol. 9, p. 33; Florence R. Sabin, *Amer. Journ. Anat.* 1909, vol. 9, p. 43; Geo. S. Huntington and C. F. W. McClure, *Amer. Journ. Anat.* 1910, vol. 10, p. 177; F. T. Lewis, *Amer. Journ. Anat.* 1905, vol. 5, p. 95; G. S. Huntington, *Anat. Anz.* 1911, vol. 39, p. 385; E. R. Clark, *Amer. Journ. Anat.* 1912, vol. 13, p. 347; G. S. Huntington, *Amer. Journ. Anat.* 1914, vol. 16, p. 259; Ch. F. W. McClure, *ibid.* 1915, No. 4; E. and E. Clark, *Contrib. to Embryology*, 1920, vol. 9, p. 447.

the capillary network of lymph vessels have fused and formed the extensive lymph sac shown in Fig. 359. In the 3rd month outgrowths from the jugular sac on each side of the neck spread and invade the tissues of the neck, head and arm—all save the central nervous system and voluntary muscles. These are not drained by the lymphatic system. The great lymph sacs are merely temporary structures; their cavities are filled by reticular lymphoid tissue produced by the lymphatic endothelium which lines the sacs. As soon as formed, the jugular lymph sac effects a union with the jugular vein, the orifice being guarded by valvular folds.

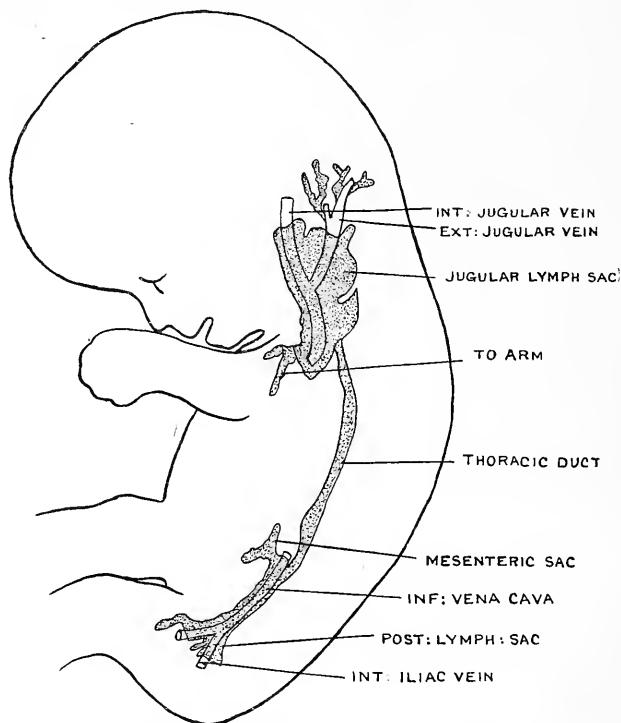


FIG. 359.—The Main Lymphatic Vessels and Sinuses of the Human Foetus at the beginning of the 3rd month. (After Prof. Florence Sabin.)

Another pair of lymph sacs appear in the pelvis—related to the corresponding iliac veins, into which they at first open (Fig. 359). From the pelvic or iliac sacs outgrowths invade the hind limbs and tissues of the pelvis and buttocks. In the mesenchymal tissue in which the dorsal aorta is embedded there appear a series of endothelial-lined lymphatic spaces, which become united and place the posterior or iliac sacs in communication with the jugular sacs. In this way two thoracic ducts are formed at the end of the second month. Two other retroperitoneal centres appear, one at the root of the superior mesenteric artery, from which arises the system of vessels which drains the alimentary tract; the receptaculum chyli is also formed from a special centre. The lymphatic

system is just as much a "closed" system as is the haemal system; everywhere its walls are lined with endothelium. Nowhere does it open on "tissue spaces."

Lymphatic Glands make their first appearance during the fourth month at the site of the lymph sacs and along the leashes of vessels leading to these sacs. They appear first as follicles which are developed within the lumina of the vessels so that the lymph passing along is exposed to the lymphocytes developed in the reticular tissue of the node. Lymphocytes arise by proliferation of the cells lining lymphatic spaces and vessels. The lymphatic glands and nodes grow in size and number during each month of foetal life. They serve as germinal centres for the production of lymphocytes.

Interscapular Gland.¹—Under this name has been included the mass of peculiar tissue which occupies the posterior triangle of the neck, and extends under the trapezius towards the posterior border of the scapula. It represents the **hibernating gland** of insectivora and bats. It begins to form in the 2nd month of foetal life at the site of the jugular lymph sac. It is composed of a stratum of three tissues—lymphoid, haemolymph (blood-forming) and fat.

Haemolymph Glands.—In the subperitoneal fat of many mammals numerous red bodies may be seen which differ from lymphatic glands in the following points: (1) the sinuses contain red blood corpuscles; (2) instead of afferent and efferent lymphatic vessels, arteries and veins open into the sinuses. They occur in the human foetus, and apparently serve the same function as the spleen (W. B. Drummond).

Bone Marrow.—Until the 5th month of foetal life the marrow is composed of branched cells embedded in a jelly-like matrix (primary marrow); it then assumes the appearance of lymphoid tissue, and contains leucoblasts; in the 6th month erythroblasts and erythrocytes appear in the dilated capillaries forming **red marrow** in the centres of ossification (Hamar). At birth the marrow of all the osseous tissue is red; during the years of active growth the marrow of the shafts of bones is gradually replaced by fat cells, **yellow marrow** being thus formed (Hutchison). From birth onwards the red marrow forms the only tissue in which red blood corpuscles are produced.

¹ For an account of this structure see Bonnot, *Journ. Anat. and Physiol.* 1909, vol. 43, p. 43.

CHAPTER XXII.

RESPIRATORY SYSTEM.

Stages in the Evolution of the Human Respiratory System.—The development of the lungs, the pleural cavities and chest wall forms one of the most complicated chapters of human embryology. The steps in the development of this system, as seen within the human embryo, are unintelligible until they are interpreted by a study of comparative anatomy, especially of those animal forms that show the manner in which a purely pulmonary system arose from one which was purely branchial. Hence it is necessary to briefly recapitulate the various modifications of the

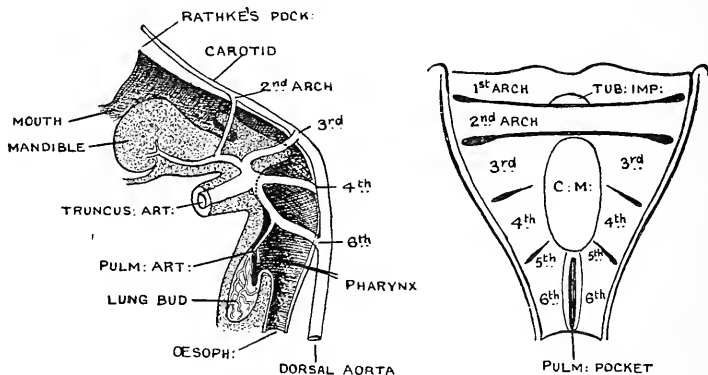


FIG. 360.—Showing the Pulmonary Artery arising from the 6th Aortic Arch in Human Embryo of 5 weeks. (After His.)

FIG. 361.—Showing that the Pulmonary Diverticulum arises between and behind the bases of the last or 6th pair of Visceral Arches. (Frazer.)

respiratory system which are seen to occur in ascending from the lowest to the highest class of vertebrates. Four stages may be recognized:

Stage I.—This stage is represented in fishes, in which the respiratory system is made up of three parts: (1) **Branchiae**, in which the respiratory exchange of blood gases is effected; (2) the swim bladder, an evagination from the oesophagus, containing oxygen, and surrounded by lymphoid tissue; (3) the musculature of the branchial arches and pharynx, which pumps water through the branchial clefts, and helps to force the blood through the branchiae; (4) nerve system with centre—both motor and sensory—in the hind-brain, and visceral nerves supplied by the vagus, and

from vasomotor centres in the dorsal region of the cord. Although branchiae are never developed in the human embryo, yet the condition in the 4th and 5th weeks, when the heart is subpharyngeal in position and the visceral and aortic arches are in process of development, can only be explained by the supposition that at one stage of evolution these parts had served a respiratory purpose.

Stage II.—In most amphibians four parts are to be recognized in the respiratory system. (1) The swim bladder is bifid; each half, now properly called a lung, projects within the abdominal cavity above the pericardium and liver (Fig. 362). (2) A respiratory passage leading from the pharynx to the lungs, and formed from the 2nd, 3rd, and 4th branchial

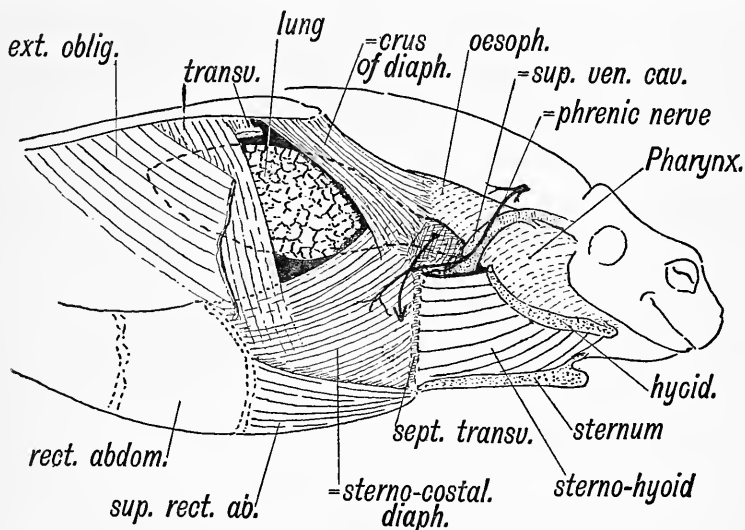


FIG. 362.—Diagram of the Lung and Respiratory Muscles of an Amphibian (Surinam toad) to show the Muscles out of which the Diaphragm is evolved. The lungs lie within the abdomen as in the 6th week embryo. The arrow, beginning over the apical region of the lung, shows the direction in which the mammalian lung develops. The shoulder girdle and greater part of the external oblique are cut away. The heart lies above the sternum.

(4th, 5th, and 6th visceral) arches. (3) The vascular system for each lung rises from the artery of the 6th visceral arch (Fig. 360). (4) The branchial muscles, which formerly forced water through the gill slits, are now transmuted into pharyngeal muscles and help to pump air into the lungs—thus acting as muscles of inspiration. The muscles of the body wall (see Fig. 362) are modified to form the muscles of expiration. Two parts of these are specially worthy of notice, because in mammals they become the diaphragm: viz. (a) part of the transversalis sheet, which rises from the spine and ends in the pericardium, oesophagus and roots of the lung; (b) a deep lamina of the rectus abdominis which ends in the pericardium. The nerve to these muscular segments descends on the outer aspect of the superior vena cava exactly in the same manner as the phrenic nerve descends to the diaphragm (Fig. 362).

Stage III.—(1) In reptiles the lungs are abdominal in position, but an elaborate series of septa have grown up within them, thus exposing a larger vascular surface to the inspired air. (2) The respiratory passage is elongated and demarcated into larynx, trachea and bronchi. (3) Ribs and sternum are developed, so that the musculature of the body wall becomes differentiated into inspiratory and expiratory muscles.

Stage IV.—In mammals an extraordinary developmental change occurs which leads to the formation of two pleural cavities and their complete separation from the abdomen by a diaphragm. The origin of the dia-

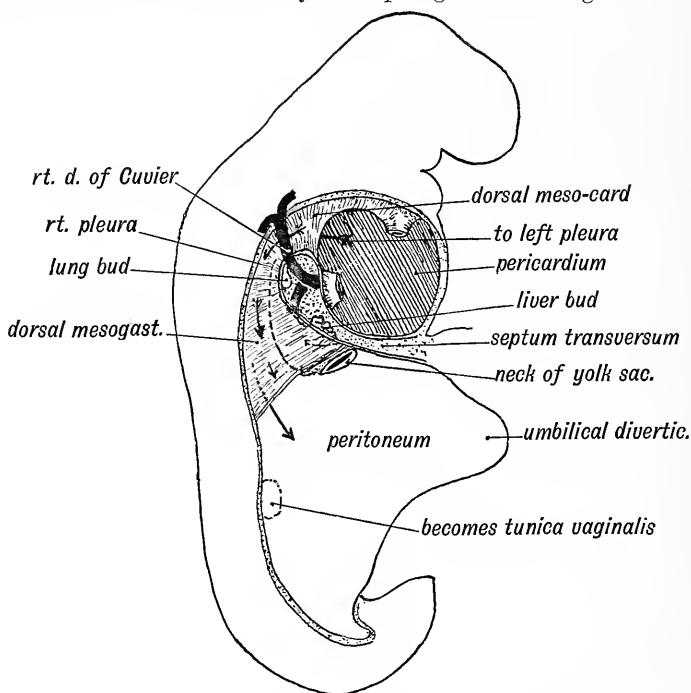


FIG. 363.—Form of the Coelom in a Human Embryo of the 5th week. The arrow under the right duct of Cuvier is in the right passage leading from the pericardial to the peritoneal cavity. It is by the expansion of this coelomic passage that the right pleural cavity is formed.

phragm must be sought for, not in the reptiles, present or past, but in a very low form of amphibian. To understand the origin of the pleural cavities and diaphragm of mammals the following points must be kept in mind : (1) That the septum transversum, in its fully developed condition, as seen in the frog, is the fibrous layer of tissue which separates the heart from the liver, a corresponding structure is seen in the human embryo. (2) Into the septum transversum are inserted the deepest layer of the rectus abdominis and vertebral fibres of the transversalis (Fig. 362). (3) The ribs are developed in the intermediate layers of the body wall—between segments of the external and internal oblique muscles. The muscular fasciculi which end in the septum transversum are deep to the ribs and intercostal

musculature. (4) The lung buds lie at first in the mesentery of the fore-gut from which they grow outwards on each side into a narrow (pleural) passage of the coelom, which leads from the pericardium to the peritoneal cavity (Fig. 363). The passage is situated at the upper border of the septum transversum; its pericardial opening, the *iter venosum*, is closed by the superior vena cava. Now, when the lung buds grow out in the mammalian embryo, they fill these passages and their hinder ends project into the abdominal cavity. Then in the 6th and 7th weeks the coelomic passage undergoes an extremely rapid expansion, growing into the body wall so as to separate the pericardium and the deeper or diaphragmatic layer of musculature from the outer or intercostal stratum. Lung growth follows closely on pleural expansion. The pleural cavities are in reality new chambers or spaces produced by an enormous expansion of the narrow coelomic or pleural passages of the embryo. We shall see that the septum transversum is also cleft during the expansion.

The development of the diaphragm gave mammals two advantages: (1) an enormous increase in the power of inspiration; (2) the respiratory negative pressure, which affects all the viscera within the body cavity in reptiles, became restricted to the thorax in mammals.

Morphological Parts of the Respiratory System are:—(a) The respiratory passage which extends from the pharynx to the bronchioles of the lung. The tissues which surround this passage are derived from the coverings and substance of the 4th, 5th and especially the 6th arch. The nasal cavities continue the breath passages to the nostrils. We have seen how these cavities are shut off from the mouth in the later part of the 2nd month. (b) The pulmonary tissue made up of (1) a diverticulum from the fore-gut which represents the swim bladder; (2) a vascular network derived from the capillaries of the fore-gut, into which opens a blood supply from the last (6th) pair of aortic arches (Fig. 360). (c) The respiratory muscles, sternum and ribs are formed in the somatopleure of the body wall.

Development of the Pulmonary System.—In the 4th week, towards the end of it, a deep groove appears in the floor of the primitive pharynx and oesophagus. The groove or trough-like depression of the fore-gut commences between the ventral ends of the 6th (or 5th and 6th, see Fig. 361) arches and stretches almost to the stomach (Fig. 364). The *furcula*, formed from the central mass and ventral parts of the 4th segments, bounds the pulmonary groove in front (Fig. 319); in its anterior part, which is the most prominent, is developed the epiglottis; the anterior parts of the lateral margins of the pulmonary groove, form the true vocal cords, for the aryteno-epiglottidean folds are secondary formations of a later date (Frazer). The posterior parts of the margins of the groove unite, and in this manner the posterior part of the groove is separated as a diverticulum on the ventral aspect of the oesophagus (see p. 270). The anterior part of the groove represents the basis of the pulmonary passage; the posterior part, the basis of the pulmonary tissue. Two points should be noted in connection with the relationships of the oesophagus at the 4th week: (1) like that of a fish, it is extremely short; (2) it lies between the right and left cavities of the coelom in the dorsal attachment of the mesocardium

of the sinus venosus (Fig. 367). (3) The part of the coelom which lies at each side of the oesophagus is the narrow passage connecting the pericardial and peritoneal cavities which becomes expanded to form the pleura.

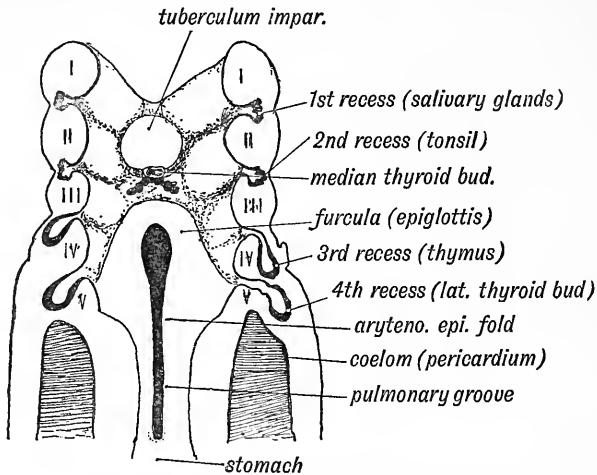


FIG. 364.—Floor of the Pharynx and Oesophagus of a Human Embryo of 4 weeks, showing the Furcula, Pulmonary Groove and Diverticulum. (After His.)

When the pulmonary outgrowth is viewed from the side, its posterior extremity is seen to end in a deep pocket, the **pulmonary pocket** or diverticulum (Figs. 276, 369). The wall of the pocket is lined by a mass of

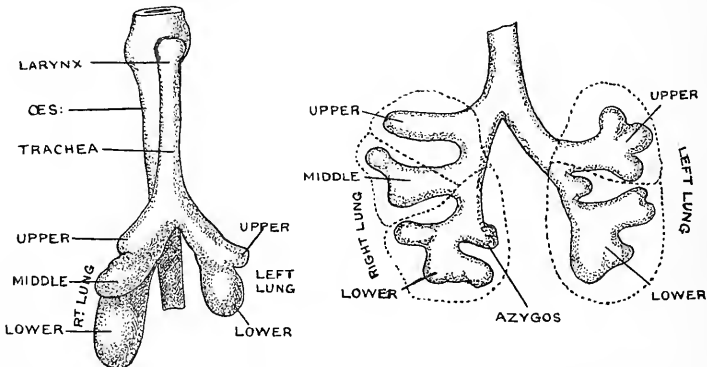


FIG. 365.—The Trachea, Bronchi and Lung Buds in the 5th week of development. (After Broman.)

FIG. 366.—The Lobulation of the Lungs early in the 6th week. (After Merkel.)

entoderm, which ultimately forms the epithelial lining of the whole respiratory tract, from the ciliated epithelium of the trachea to the pavement epithelium lining the alveoli of the lungs. Round the pulmonary bud is grouped a mass of mesodermal tissue out of which the connective-tissue system of the trachea, bronchi and lungs is developed.

In the 5th week the pulmonary pocket produces a larger right and a smaller left process, the right and left **lung buds** (Fig. 365). The median part of the pulmonary outgrowth separates from the pharyngeal floor and forms the trachea. The anterior part forms the larynx (see p. 351). The right bud forms the right lung and bronchus; the left, the left lung and bronchus. As the pleural cavities and their contained lung buds develop the stomach is forced backwards; the oesophagus becomes elongated. The tracheal part of the bud becomes separated from the oesophagus, but both retain the same nerve supply—the recurrent branch of the vagus—which is the nerve of the 6th arch. The rapid development of the lung during the 4th, 5th, and 6th weeks is illustrated by Figs. 276, 277, 365, 366. In the 4th week the lung bud is a mere diverticulum;

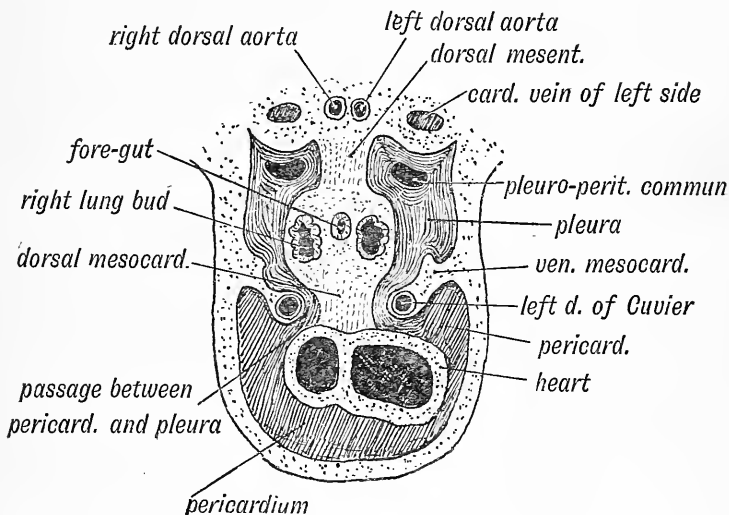


FIG. 367.—A Section of a Human Embryo to show the Relationships of the Pulmonary Buds at the 5th week, looking backwards. (After Kollmann.)

in the 5th the trachea and buds of the main bronchi are apparent; in the 6th week the secondary bronchi and separate lobes are in a process of differentiation.

In Fig. 367 the relationship of the lung buds is shown to surrounding structures during the 5th week. The following points should be noted:

(1) As the lung buds grow out they push their way into the **pleural passages**—the narrow communications between the pericardium and peritoneum. These parts of the coelom form the **pleurae**. The part of the coelomic lining which is invaginated as a covering on the lung bud becomes the visceral pleura. The invaginating or ensheathing lining of the isthmus becomes the parietal pleura. As the lung buds grow, they distend the originally small pleural parts of the coelom until at the time of birth the right and left pleurae almost meet in front of the heart, and completely separate the chest wall from the pericardium and diaphragm.

They meet after birth under the sternum, enclosing between them the anterior mediastinum.

(2) As will be seen from Fig. 363, the lung buds sprout out from the mesentery just behind the duct of Cuvier. This relationship is retained in the adult, the vena azygos major and superior vena cava lying above and in front of the root of the right lung. The roots of the lungs represent the situation at which the embryonic pulmonary outgrowth took place. If the left duct of Cuvier persisted it would lie above and in front of the root of the left lung. The ductus arteriosus—part of the 6th arch—lies over the root of the left lung. At this stage (5th week) the pleural passage or cavity is still in communication with both pericardial and

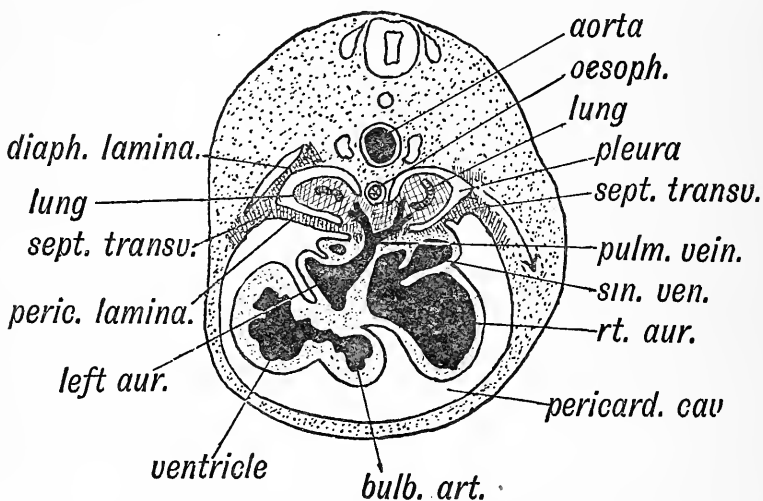


FIG. 368.—Transverse Section of a Human Embryo showing (1) the Outgrowth of the Lung Buds from the Mesentery of the Fore-gut; (2) the Separation of the Pericardium from the Body Wall and Formation of the Pleural Cavities; (3) the Separation of the Diaphragmatic Lamina from the Septum Transversum. The arrow shows the direction in which the left pleura invades the body wall. (After Lockwood.)

peritoneal cavities. Its communication with the pericardium closes at the end of the 6th week.

Formation of the Bronchi and Lungs.¹—The bronchi are the stalks of the right and left lung buds. The right bud is the bigger; the left is probably repressed by the heart turning to the left side. The right shows three secondary buds—the forerunners of the upper, middle and lower lobes of the lung; the left, two, which form the upper and lower lobes (Fig. 365).

The condition of the lung buds during the 6th week is shown in Figs. 366, 370. Not only are the right and left bronchi formed, but so also are the chief bronchial ramifications. Each ramification ends in a bud, which divides again and again and keeps on dividing until the fourth month. The terminal buds form the bronchioles and infundibula. Each bud is

¹ R. Heiss, *Anat. Anz.* 1912, vol. 41, p. 62 (Dev. of Lobes of Lung).

solid, and carries its sheath of mesoderm; the appearance on microscopic examination is very similar to that of a gland, such as the pancreas or parotid. In the 3rd month the mesoderm between the pulmonary buds is extremely abundant; by the sixth month it forms merely a thin stroma amongst the alveolar air sacs. At the sixth month saccular evaginations occur from the infundibula; they form the air cells, or alveoli. Nothing is known definitely of the growth of the lung tissue after birth, but it is probably formed by outgrowths from the infundibula occupying the sub-pleural layer. The opinion usually held by embryologists is that the production of new alveoli ceases at the 7th month of foetal

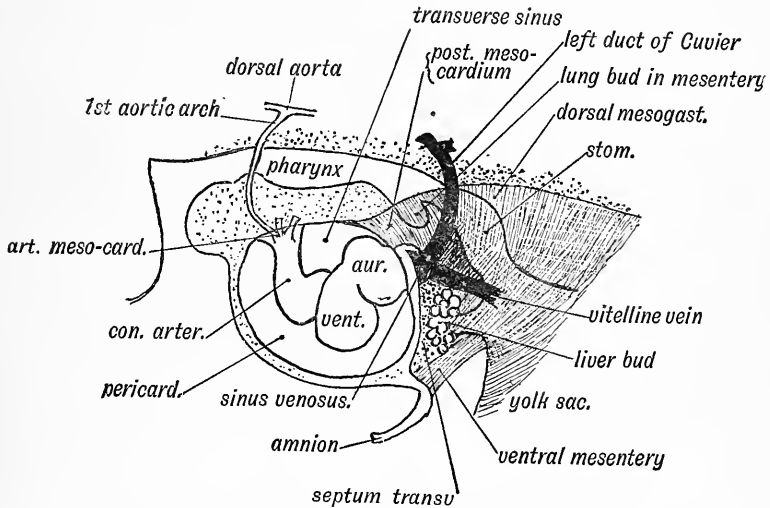


FIG. 369.—Diagram to show the manner in which the Heart is fixed within the Pericardium by the Arterial and Venous Mesocardia in a Human Embryo of 4 weeks. The "dorsal mesocardium" in the above figure forms part of the venous mesocardium.

life. After that time there is merely an enlargement of the elements already formed.

Changes in the Shape of the Lung.—Even in the 6th week the lungs are merely glandular masses round the terminal parts of the bronchial outgrowths. As in the frog, the hilum at this time forms the apex of the lung. During the 2nd and 3rd months the lungs assume their definite shape. The upper lobe grows towards the neck, and an apical region is thus formed. The diaphragmatic or basal surface is at first absent, but as the pleural cavities expand and the basis of the diaphragm is stripped from the body wall, this surface appears. In the human and anthropoid foetus the diaphragmatic or basal surface becomes remarkably large. The most important change, however, relates to the anterior or ventral border of the lungs; at first situated on the dorsal side of the pericardium the lungs expand forwards until they reach almost to the lateral borders of the sternum. In man and anthropoids the ventral or sterno-costal part of the lung reaches a high degree of development.

Evolution of Air Sacs.—In reptiles we see the original bladder-like lung becoming demarcated into two parts—an anterior or cephalic part with thick spongy walls which contain cellular recesses for air and are richly supplied with blood; and a posterior, thin-walled and simple part. The thin-walled hinder part serves as a pulmonary bellows during the respiratory expansion and contraction of the body wall; it naturally acts on the most yielding part of the lung. In birds, the anterior or respiratory part of the lung has been sharply demarcated from the posterior or “bellows” part. The latter is broken up into abdominal air sacs. In mammals the “bellows part,” represented by the pulmonary infundibula and air sacs, is disseminated amongst the “respiratory” tissue and the bronchi are arranged in such a way as to permit every part of the lung to undergo expansion. Thus the pattern of the bronchial tree is determined by the

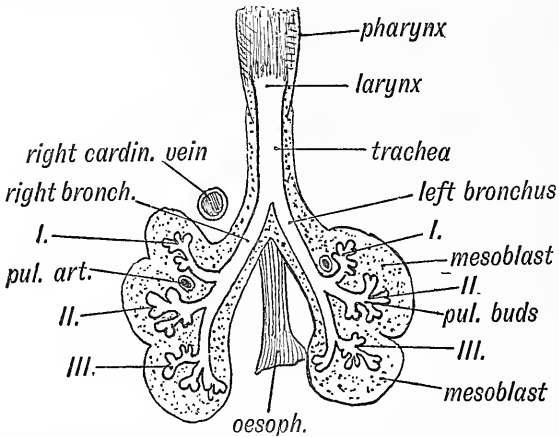


FIG. 370.—The condition of the Right and Left Pulmonary Buds in an Embryo at the end of the 6th week. (After His.)

nature of the respiratory movements. Whereas only the respiratory part of a bird's lung is supradiaphragmatic the whole of the mammalian lung occupies this position.

There are certain **peculiarities in the lungs** of animals which are adapted to an upright posture (Man and Anthropoids):

(1) **Ramification of the Bronchi.**—In quadrupedal mammals the main bronchus passes backwards in the lung as a main stem, which grows gradually smaller by giving off four dorsal and four ventral bronchial branches (Fig. 371). So altered are the human lungs, that the arrangement of bronchi seen in most mammals is not easily recognized in them. The ventral bronchi are larger, longer and more branched than in other mammals. In the human as in the mammalian lung the secondary and terminal bronchi are developed by a dichotomy or subdivision of the pulmonary buds.

(2) **The Lobes of the Lungs.**—In the embryonic condition (Fig. 370) it is seen that the right and left lung buds are nearly symmetrical. Aebys supposed the upper lobe of the right lung to be absent in the left;

and this is also the conclusion which Flint arrived at after a minute investigation of the development of the lungs of the pig. It must be remembered that the point of origin of any bronchus may easily be moved to meet new physiological conditions. At least in the human embryo each main bronchus gives off three primary buds. All three remain separate on the right side; on the left the upper and middle primary buds arise together (Fig. 370). Hence the upper lobe of the left lung represents the upper and middle lobes of the right. In the sheep and pig the upper right lobe springs from the trachea. The bronchus of the upper right lobe (the reason for it is not clear) commonly lies above its artery—that is to say, it is **eparterial**. The other bronchi are **hyparterial**. A clue to the asymmetry of the right and left lungs will be found in a fuller knowledge of the mechanism of respiration.¹

† (3) **The Diameters of the Thorax.**—The peculiar branching of the bronchi in man and upright primates is due to the shape of the lungs,

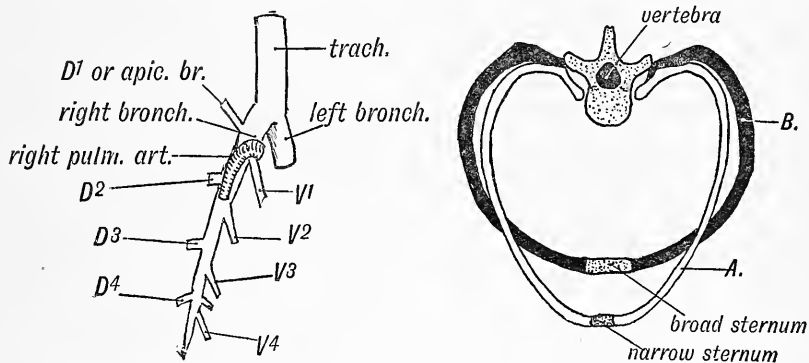


FIG. 371.—Scheme of the Bronchial Ramifications in Quadrupedal Mammals. *D*, the dorsal ramifications; *V*, the ventral ramifications.

FIG. 372.—Diagrammatic Section of the Thorax of a Quadrupedal Mammal (*A*), contrasted with a corresponding section in Man (*B*).

which in turn is due to the shape of the thorax. In quadrupedal animals, such as the horse or dog, in which the chest rests and is supported between the fore limbs, the thorax has its greatest diameter in the dorso-ventral direction (Fig. 372). In upright animals (man, anthropoids, and also in some water living mammals, such as seals, etc.) the transverse diameter becomes the greater. At birth the diameters of the child's thorax are nearly equal. The thorax is flattened by the spine becoming invaginated within it; the thorax thus comes to lie within the axis of gravity of the upright body.

(4) **The Azygos Lobe.**—On the inner side of the right lung of man the azygos lobe is frequently present, sometimes as a mere pulmonary projection or trace, sometimes as a lobule. It represents an over-development of the second ventral branch from the right bronchus (Fig. 366). It

¹ Any one interested in this problem should consult Prof. Huntington's paper, *Amer. Journ. Anat.* 1920, vol. 27, p. 99.

projects into and fills a slight recess between the pericardium and diaphragm, behind the intra-thoracic part of the inferior vena cava. This lobe is always well developed in quadrupedal mammals. In them the pericardium is separated from the diaphragm by a diverticulum of the right pleura—the **sinus subpericardiacus** (Fig. 374). With the assumption of the upright posture (in man and anthropoids) the mechanism of respiration has become altered and the heart sinks until it rests on the diaphragm, the subpericardiac sinus and azygos lobe being thus obliterated. The reappearance of the azygos lobe as a separate structure—for a buried rudiment is always present—in man is an *atavism*—that is to say, a recurrence of an ancestral feature. In quadrupeds the contraction of the diaphragm

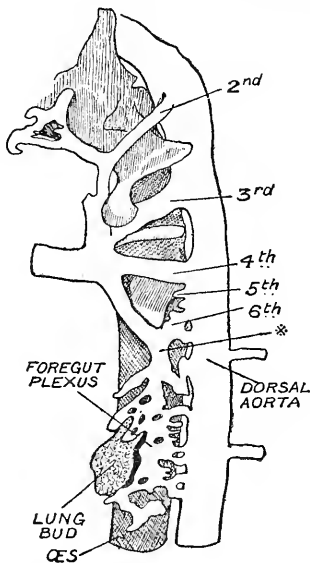


FIG. 373.—Showing the Origin of the Blood Supply to the Lung, in Cat Embryo. (Huntington.)

is followed by an expansion of the lobus azygos and a corresponding elongation of the highly elastic intra-thoracic part of the inferior vena cava; in man, on the other hand, the contraction of the diaphragm is followed by a descent of the heart, thus indirectly enlarging the pulmonary space.

Blood Supply of the Lung.¹—The pulmonary aorta is formed with the ascending part of the aortic arch, out of the truncus arteriosus (see p. 249). The right and left pulmonary arteries spring as branches from the right and left 6th aortic arches (Fig. 373). The lung buds are at first supplied by arteries arising from the dorsal aorta (Huntington), but in the 5th week this primary pulmonary plexus is joined by a communication

¹ J. L. Bremer, *Amer. Journ. Anat.* 1901, vol. 1, p. 137 (Dev. of Pulmonary Arteries); V. Federow, *Anat. Hefte*, 1910, vol. 40, p. 529 (Dev. of Pulmonary Veins); Geo. S. Huntington, *Anat. Rec.* 1919, vol. 17, p. 165.

from the 6th aortic arches, this anastomosis being the basis of the pulmonary arteries (Fig. 273). At first the pulmonary arteries descend by the side of the trachea, but as the heart becomes intra-thoracic in the 6th and 7th weeks they are gradually shortened until they pass horizontally to the roots of the lungs. The pulmonary veins grow out from the pulmonary buds and enter the left auricle through the venous mesocardium about the 5th week (Fig. 368). The mesenchymatous or interstitial tissue of the lungs is supplied by the bronchial arteries which represent the primary vessels of the lung buds (Fig. 373). These arteries also supply the pleura on the mediastinal and diaphragmatic surfaces of the lungs.

Changes at Birth.—When the child begins to breathe at birth, the expansion of the lungs opens up the pulmonary circulation; the foramen ovale is closed and the ductus arteriosus begins then to be closed, and within the 1st month becomes reduced to a fibrous cord. The ductus arteriosus

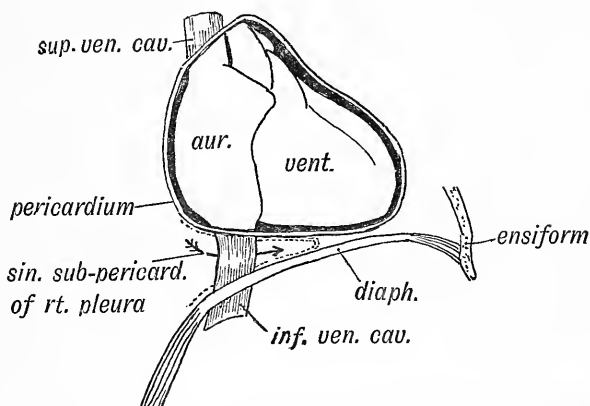


FIG. 374.—The Relationship of the Heart to the Diaphragm in Quadrupedal Mammals.

represents the dorsal segment of the 6th left arch; the corresponding part of the 6th right arch disappears soon after it is formed. It is not until about the 4th day after birth that the whole of the lung is inflated. The first part to expand is the costo-sternal or ventral part; the second, the diaphragmatic or basal part, the apex is the third, and the dorsal border and deep part the last.¹

The Larynx.²—The larynx is developed round the anterior part of the pulmonary diverticulum. The origin of the cartilages of the larynx is shown in Fig. 375. The thyroid cartilage is formed by the expansion and amalgamation of the skeletal bases of the 4th and 5th visceral arches; at least this is true of lower mammals, but in higher mammals only the 4th

¹ For papers relating to the morphology and mechanism of the lungs see *Further Advances in Physiology*, edited by Leonard Hill, 1909; also Keith, *Journ. Anat. and Physiol.* 1905, vol. 39, p. 243.

² J. E. Frazer, *Journ. Anat. and Physiol.* 1910, vol. 44, p. 156; H. Lissner, *Amer. Journ. Anat.* 1911, vol. 12, p. 27; F. H. Edgeworth, *Quart. Journ. Mic. Sc.* 1916, vol. 61, p. 383.

is involved (Edgeworth). The skeletal basis of the 6th or pulmonary arch in man, which forms the two lateral cartilages in the short pulmonary passage of the frog, becomes divided into a dorsal segment which forms the arytenoid cartilage, a ventral segment to form the cricoid. From the posterior part of the primitive lateral cartilage arise the rings in the wall of the trachea, chief, secondary and ultimate bronchi (Fig. 375).

Prof. Frazer has made a very thorough investigation of the development of the larynx. At each side of the primary pulmonary orifice lies a mass of tissue representing the last or 6th visceral arch (Fig. 361). In this tissue develops the various parts of the larynx. The cricoid and arytenoid are the primary cartilages; they are the only ones present in the larynx of amphibia and reptiles. The thyroid only appears in mammals. The true vocal cords represent the primary opening of the larynx. In the 2nd

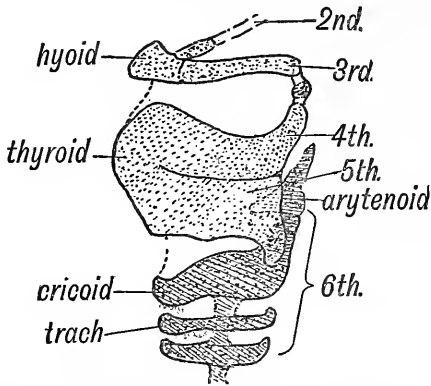


FIG. 375.—Diagram of the Cartilages of the Larynx to show the parts derived from the Skeleton of each Visceral Segment.

and 3rd months of human development the part of the laryngeal cavity above the vocal cords (suprarimal part) is produced by the upgrowth of the lateral masses on each side of the primary opening. In these masses are developed the arytenoid cartilages and the aryteno-epiglottidean or permanent folds which bound the lateral margins of the secondary laryngeal orifice. The epiglottis, in Prof. Frazer's opinion, is developed out of the mass of tissue (central mass) which lies behind the 2nd and 3rd arches (Fig. 361).

The muscles within the larynx are derived from the 6th visceral segment and are supplied by the inferior laryngeal nerve, while the crico-thyroid arises from the musculature of the 4th segment. In fish the pharyngeal orifice of the oesophagus is guarded and kept shut by a sphincter made up of striated muscle. When a pulmonary system is evolved the laryngeal or guarding musculature is derived from the primary sphincter of the oesophagus (Edgeworth).

The epiglottis is developed in the furcula (Symington); in lower vertebrates its lateral margins extend into the aryteno-epiglottic folds. The cartilages of Santorini and Wrisberg, in the aryteno-epiglottic folds, are continuous with the epiglottis in many mammals (Sutton). Until the 5th

month of foetal life the epiglottis lies behind the palate and within the naso-pharynx—a position which is normal for the adults of many kinds of mammals.

The purposes which the larynx serves in all air-breathing vertebrates are (1) to regulate the inflow and outflow of respiratory air, and thus the positive and negative pressure within the lungs; (2) to prevent food passing into the air passage. The production of voice which has led to a marked alteration of the human arytenoid cartilage is a secondary function. Only in man and the higher anthropoids are the true vocal cords covered by stratified epithelium; but all the muscles of the human larynx are represented in the larynx of the ape, although in a less specialized condition.¹

Soon after the upgrowth of the lateral masses to form the suprarimal cavity of the larynx, an evagination takes place above each vocal cord to form the ventricles. In the 5th month mucous glands are developed from the membrane lining the ventricles, and a little later an outgrowth is developed from their apices to form the saccules of the larynx. They project against the thyro-hyoid membrane. Occasionally the **saccule** of the larynx may protrude through the thyro-hyoid membrane, thus giving rise to an air cyst in the neck. Laryngeal air-sacs are normally developed in anthropoids after birth, and attain a great size in the adults, extending to the chest and axillae. Their function is unknown.

Diaphragm.²—The diaphragm constitutes one of the most pronounced structural characteristics of mammals. The ancestral mammalian types in which the diaphragm first appeared are long since extinct; we cannot study the evolution of the diaphragm among modern vertebrates. There are certain facts which throw light upon its origin, and make us certain that the diaphragm did not rise up gradually as a partition within the coelom and shut off that part which contains the lungs from the part containing the abdominal viscera. During the 4th and 5th weeks of development the pleural cavities are represented merely by the two short passages leading from the pericardial to the peritoneal cavity. In the 5th week the passages lie in the cervical region under the 4th and 5th spinal segments, from which the phrenic nerve arises, and from which the musculature of the diaphragm is derived. It is clear, then, that the diaphragm entered into the service of the lungs when these were situated, as in the frog, below the cervical region (Fig. 362). In some manner, as the lungs developed and afterwards took up a thoracic position, the muscle which became associated with them in the neck accompanied them when they retreated to their new position in the thorax. If we are to find a representative of the early form of the diaphragm, it must be amongst amphibians that we should look. We can also get

¹ W. H. Duckworth, *Journ. Anat.* 1913, vol. 47, p. 82.

² See Keith, *Journ. Anat. and Physiol.* 1905, vol. 39, p. 243; Mall, *Bull. Johns Hopkins Hosp.* 1901, vol. 12, Nos. 121-123, pp. 158, 171; I. Broman, *Ergebnisse der Anat.* 1911, vol. 20, p. 1; A. Brachet, *Mém. de l'Acad. Roy. de Med. de Belgique*, 1906, vol. 19; R. Mazilier, *l'Embryologie du Diaphragme*, Lille, 1907; Gladstone and Cockayne, *Journ. Anat.* 1918, vol. 52, p. 64.

light on its origin by studying certain malformations to which it is liable in man.

In Fig. 376 is shown the thoracic aspect of the diaphragm of a newly born child, in which the left **pleuro-peritoneal opening** has remained patent. Through the opening the upper end of the left supra-renal body and the spleen projected within the pleural cavity, giving rise to a congenital diaphragmatic hernia. The pleuro-peritoneal opening is situated on each side, between the muscular fibres which rise from the ribs and sternum, and which form the **ventro-lateral part** of the diaphragm, and the muscular fibres which arise from the spine and arcuate ligaments, forming the

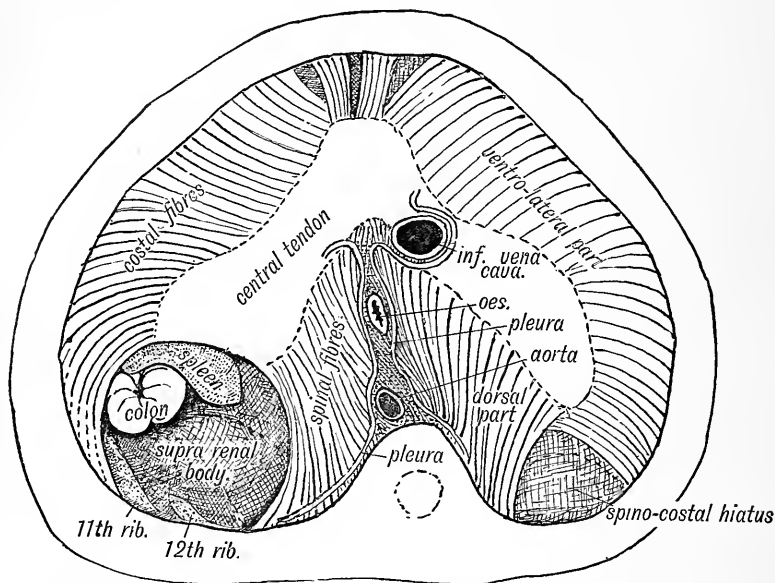


FIG. 376.—The Thoracic Aspect of the Diaphragm of a newly born Child in which the communication between the Peritoneum and Pleura has not been closed on the left side; the position of the opening is marked on the right side by the Spino-costal Hiatus. The dorsal mesentery of the fore-gut (represented by the posterior mediastinal pleura) is also shown.

dorsal part of the diaphragm. The phrenic nerves, when they reach the diaphragm, divide into two branches, a ventral to the right and left ventro-lateral parts (from 3rd and 4th cervical nerves), and a dorsal branch (from 4th and 5th cervical nerves) to the right and left dorsal parts. The central tendon, situated between the four parts just mentioned, makes up the fifth morphological element of the diaphragm. Each of these five parts—the central, the two dorsal and two ventro-lateral, has its own developmental history.

The **central tendon of the diaphragm** is formed from the septum transversum (Fig. 377). The manner in which that structure is cleft into its pericardial and diaphragmatic elements by the outgrowth of the two pleural passages and lung buds has been already described (p. 342). The dorsal and ventral mesentery of the fore-gut (Fig. 379) are included in the

formation of the septum transversum (p. 272), and hence the structures developed in these mesenteries—the aorta, oesophagus, azygos veins, thoracic duct, vagus nerves and inferior vena cava—perforate the median or central part of the diaphragm. The structures of the posterior mediastinum lie in the mesentery of the fore-gut (see Figs. 376, 378).

The **ventro-lateral parts** of the diaphragm are derived from the ventral longitudinal muscular sheets which give rise to the rectus abdominis and depressors of the hyoid bone (Fig. 362). Were the parts of this sheet restored to their embryonic relationships, then the pericardium should be placed beneath the mandible, so that the central tendon of the diaphragm lies opposite the 4th cervical segment. The sternal and costal origins of

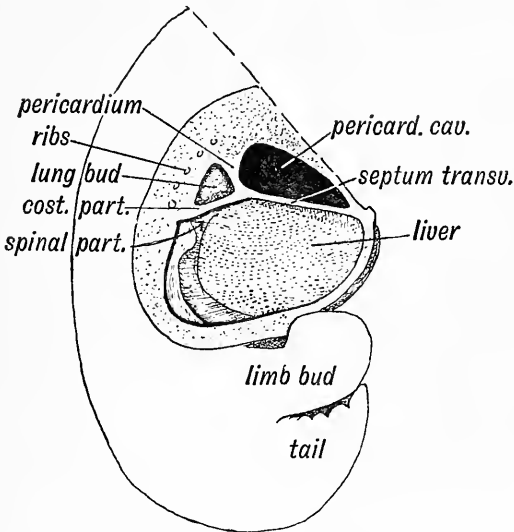


FIG. 377.—A Lateral Section along the Thoracic and Abdominal Regions of a Human Embryo in the 5th week of development, showing the Lung Bud growing within the Septum Transversum and separating it into a Pericardial and a Diaphragmatic (costal) Lamina. The arrow points to the dorsal mesentery of the fore-gut within which the crura of the diaphragm are developed. (After Mall.)

the ventro-lateral segment of the diaphragm should be detached in the thorax and the muscle placed ventrally in the neck so that it is continuous, at its insertion to the septum transversum, with the depressors of the hyoid bone. Behind the detached thoracic origins of the sternal and costal fibres should become continuous with the anterior end of the rectus sheet. In the human body the anterior part of the rectus sheet becomes divided into four strata—(1) the ventro-lateral fibres of the diaphragm, (2) the interchondral parts of the intercostals, (3) the rectus abdominis, which in all mammals, except man and the anthropoids, reaches forwards to the 1st rib, (4) the pectoralis major, minor, subclavius and that frequent human abnormality—the **sternalis** muscle. The development of the lung separates the deepest part of the rectus sheet from the chest wall to form the ventro-lateral part of the diaphragm. The ribs are formed in

the chest wall and to the posterior six, this part of the diaphragm ultimately obtains an origin.

The **dorsal parts of the diaphragm** are formed from that part of the transversalis sheet of the body wall which forms the subvertebral musculature (Figs. 362, 376). The manner in which these parts of the diaphragm are detached from the body wall and carried into the thorax by the developing pleural cavities and lungs is shown in Figs. 377, 378. The right and left spinal parts of the diaphragm sink within the dorsal mesentery of the fore-gut, obtaining anteriorly an insertion to the pericardium and septum transversum, while posteriorly they retain an origin from the spine and costal processes. The quadratus lumborum, longus colli, the rectus

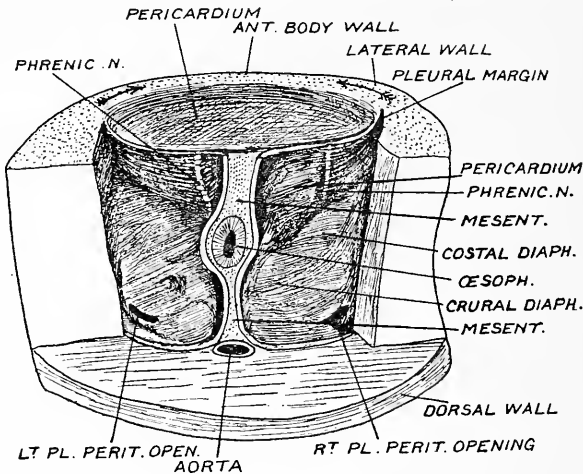


FIG. 378.—A Dorsal View of the hinder parts of the Expanding Pleural Cavities in a Human Foetus 16 mm. long and in the 7th week of development. (After Gladstone and Cockayne.) The pleuro-peritoneal openings are at the point of closure. Compare with Fig. 376. Arrows show the direction in which the Pleural Cavities expand into the Body Wall and separate the Pericardium from the Thoracic Parieties.

capitis anticus major and minor are also derived from the subvertebral musculature.

Pleuro-peritoneal Openings.—The pleural passages, into which the lung buds develop at the end of the first month, open into the pericardium by the *iterinera venosa*; behind they communicate with the peritoneum by the pleuro-peritoneal openings (Figs. 329, 330). These lie above the septum transversum (Fig. 379) and are separated by the mesentery of the fore-gut. In the mesentery between the openings are developed the spinal fibres of the diaphragm; on the lateral side of each opening arise the costal fibres. The condition of the pleuro-peritoneal openings in the 7th week when they are on point of closing, is shown in Fig. 378. The actual closure is effected by that form of embryological healing to which the name of *zygosis* has been given (p. 287), but certain accessory factors are also involved in approximating their margins. (1) The spinal fibres migrate outwards and obtain attachment to the arcuate ligaments; the

costal fibres migrate inwards, obtaining an origin from the 11th and 12th ribs. Only in man and anthropoids does this migration occur, and the extent to which they approach each other and thus close the opening is extremely variable. (2) The collapsed condition of the lungs allows the abdominal viscera, developed in the domes of the diaphragm, to press the spinal and costal fibres against the dorsal wall of the thorax, thus mechanically closing the aperture. The liver, especially, by its upgrowth within the septum transversum helps to close the apertures, particularly on the right side, which is seldom the site of a diaphragmatic hernia. The supra-renal bodies are also developed just behind the pleuro-peritoneal

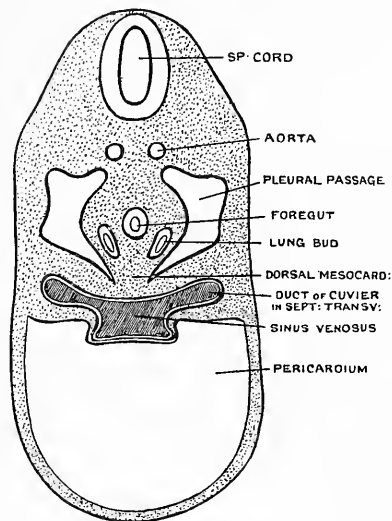


FIG. 379.—Section across Mesentery of the Fore-gut to show its relationship to the Pleuro-peritoneal Openings and Septum Transversum.

orifices, and help to close them. Indeed, the mesentery of the Wolffian body, in the anterior extremity of which the supra-renal bodies develop, are attached along the dorsal wall of the coelom as far as the septum transversum, where it forms a fold upon the lateral or outer margin of the pleuro-peritoneal orifice. The developmental representative of this mesentery is sometimes named the pleuro-peritoneal membrane, and is regarded as an embryonic form of diaphragm.

Musculature of the Body Wall.—The development of the musculature of the body wall, also of the ribs and sternum, ought rightly to be included here, for all are closely related to the mechanism of respiration. The ribs have been already considered, and it will be more convenient to reserve the development of the wall of the thorax and abdomen with other correlated structures for another chapter (Chap. XXV.).

CHAPTER XXIII.

UROGENITAL SYSTEM.

Evolutionary Stages.—The association of the genital with the urinary system has to be sought for in the ancestry from which vertebrate animals arose, for even in the lowest vertebrates they are already associated. The evidence of embryology makes it certain that man has been evolved from a type in which each segment of the body was provided with its own excretory tubule or kidney. The parts of an excretory or **nephric tubule** are diagrammatically represented in Fig. 380, *A*. Into its dilated

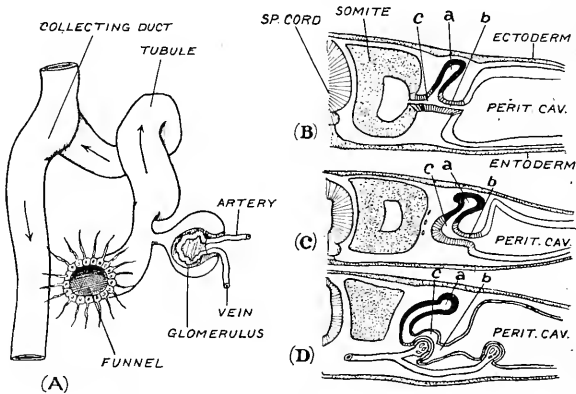


FIG. 380.—Composition and Origin of Nephric Tubules.

A, Diagram of an Isolated Nephric Tubule. (After Semon.)

B, Showing the manner in which the Intermediate Cell Mass (*a*, *b*, *c*) gives origin to the Nephric Tubule (*a*), Peritoneal Funnel (*b*) and the Nephrocele (*c*).

C, The isolation of these parts from the Somite and their union to form a system.

D, The Origin of a Glomerulus in the Wall of the Nephrocele (*c*). (After Felix.)

head or beginning projects a vascular body—a **glomerulus**—similar to the glomeruli of the kidney; at its commencement the tubule is also connected with the peritoneal cavity by an open funnel-shaped structure—the **peritoneal funnel**. By this communication ova or spermatozoa, which are shed from the genital glands, may escape from the peritoneal cavity and enter the excretory tubules, and thus pass outside the body. We shall see that the openings by which ova still escape in women and the passages by which semen leaves the testicle in men, are derived from the

funnel elements of the nephric tubules. The essential part of the excretory organ is the epithelial-lined wall of the tubule itself. The secretion of the tubules is conveyed to a common collecting duct—the **nephric duct**—which ends in the cloaca.

An inspection of Fig. 380 (*B, C, D*) will show how the various parts of the nephric tubule just named arise from the wall of the intermediate part of the coelom. We have already seen (p. 41) how the mesoderm on each side of the embryo becomes demarcated transversely into body segments or somites, and also longitudinally into the paraxial mass, the intermediate cell mass and the parietal laminae, and how extensions of the coelom are included in each of these longitudinal divisions. From Fig.

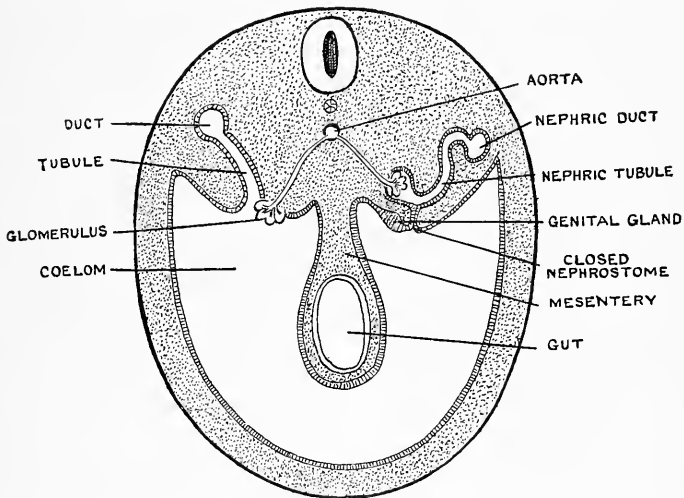


FIG. 381.—Schematic Section to show the Specialization of the Dorsal Part of the Coelom into Nephric Tubules, Peritoneal Funnels and Glomeruli. On one side the tubule is connected with the peritoneal cavity by an open funnel while the Glomerulus is intraperitoneal as is usual in pronephric tubules; on the other side they are buried in the Wolffian or intermediate ridge.

380 it will be seen that a nephric tubule arises by an evagination of the outer wall of the intermediate part of the coelom, while the glomerular chamber or nephrocele (*c*) and the peritoneal funnel, are produced from the coelomic passage which originally connected the peritoneal cavity with the cavity of a somite (Fig. 380). Thus the nephridial and genital systems must be regarded as modified parts of the wall of the original coelomic cavity.¹

Succession of Renal Systems.—In the evolution of the higher vertebrates there has been a succession of three renal systems, the third being, the present functional system—the *kidneys* or *metanephros*. All of them—**pronephros**, **mesonephros** or **Wolffian body** and **metanephros**, are compounded of the same system of nephridial elements just as the milk and

¹ See W. Felix, *Keibel and Mall's Manual of Human Embryology*, vol. 2, 1912; Eliz. A. Fraser, *Journ. Anat.* 1920, vol. 54, p. 287; Gyneth Buchanan and Eliz. Fraser, *ibid.* 1919, vol. 53, pp. 35, 97; F. T. Lewis, *Amer. Journ. Anat.* 1919, vol. 26, p. 423; J. L. Bremer, *ibid.* 1916, vol. 19, p. 179.

permanent teeth are successive manifestations of the same dental system. In the human embryo of the 6th week all three systems may be seen; while the pronephric system, which is developed in the last four or five cervical segments and first two or three thoracic, is then undergoing retrogression, the metanephric in the hinder lumbar segments is only appearing; in this week the mesonephric system is approaching the height of its development, extending from the 5th cervical to the 3rd lumbar segment.

It is clear that pronephros, mesonephros and metanephros are parts of the same linear series of organs. All are made up of nephric tubules opening into a common excretory (Wolffian) duct. While in the cervical region the tubules are simple and retain their segmental arrangement, in the

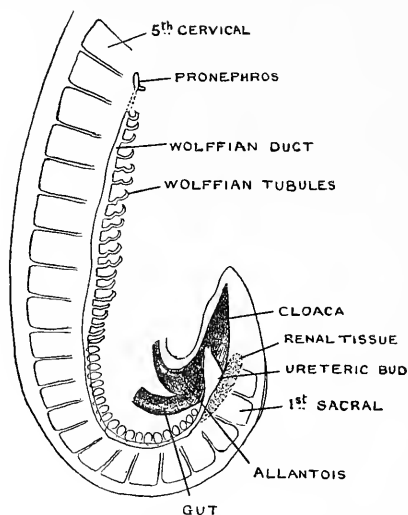


FIG. 382.—Condition of the Nephric or Renal System in a Human Embryo of 4 weeks. (After Ingalls.)

dorsal and lumbar region they multiply in number and complexity; in the sacral region they become exceedingly numerous and massed round a diverticulum from the Wolffian duct—which forms the primitive ureter. In the second month of human development the Wolffian body is at the height of its development; in the 3rd month the permanent kidney assumes its predominant position, and its predecessor—the Wolffian body—is converted into a mere appendage of the genital system.

The Wolffian Body or Mesonephros (Fig. 382).—In lower vertebrates (Fishes and Amphibians) the Wolffian body is the functional kidney; in higher vertebrates (Reptiles, Birds, and Mammals) it is merely a temporary or embryonic structure, the renal function being taken over by the permanent kidney. Apparently the permanent kidney (metanephros) arose by a hypertrophy and separation of the hindermost segment of the Wolffian body. The presence of the mesonephros in the human embryo and in the embryonic stages of the three great classes of higher vertebrates,

with the presence of many curious stages in the development of their genito-urinary system, can be explained only by the fact that these higher forms are descended from ancestors of the lower.

In Fig. 383 is given a diagrammatic representation of the tubular composition of the Wolffian Body of the frog, which in many points corresponds to the same structure in the human embryo. Each body is made up of a main duct and a series of tubules. In the frog, as in the human embryo, the hind-gut ends in a dilatation, the **cloaca**. In the cloaca open the rectum, allantois or bladder, and the two **Wolffian ducts**—right and left. In the frog, the Wolffian bodies lie on each side of the spine, their anterior ends reaching forwards to the region of the heart. Each duct is joined

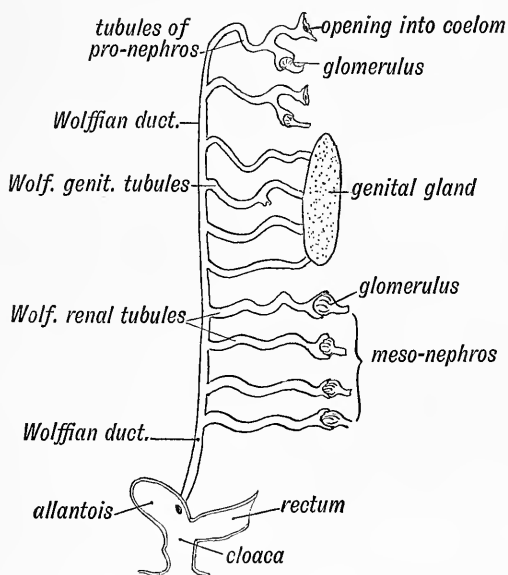


FIG. 383.—Scheme of the Wolffian Body of the right side.

by numerous convoluted tubules—the **Wolffian** or **Nephric tubules**. Each tubule is furnished with a glomerulus at its blind extremity, and in most features agrees with a secretory tubule—such as is seen in the permanent kidney. These tubules secrete the urine; the Wolffian duct conveys the urine from the tubules to the cloaca. The anterior tubules, however, lose their secretory function and become associated with the genital gland. In the male frog they convey the spermatozoa to the Wolffian duct, which thus carries both urine and spermatozoa. In the female, the **genital** Wolffian tubules are connected with the ovary but are quite functionless (Fig. 383).

The Wolffian Body in the Human Embryo.—By the middle of the second month of foetal life, the Wolffian body is well developed; by the end of that month it is undergoing a process of atrophy, except those parts connected with the genital organs. Originally extending from the

5th cervical to the 3rd lumbar segment, by the 8th week it is confined to the region of the lower three thoracic and upper three lumbar vertebrae where it projects at the dorsal attachment of the mesentery (Fig. 384). Its anterior end lies at the pleuro-peritoneal orifice of the diaphragm. To its inner side, in the lower dorsal region, lies the **genital ridge**. The genital and the Wolffian bodies have each its own mesentery, but these two mesenteries have a common attachment—the common urogenital mesentery (Fig. 384). On section the Wolffian ridge is seen to be made up of convoluted tubules terminating at their blind extremities in glomeruli. The tubules open into the Wolffian duct, just as in the frog; the duct is situated on the lateral margin of the ridge, dorsal to the Müllerian duct. It runs back-

wards in this ridge and turns into the pelvis to end with the Müllerian duct (also situated in the Wolffian ridge) in the cloaca of the hind-gut (Fig. 382). The whole arrangement is similar to that seen in the frog. Further, as in the frog, certain of the more anterior or genital tubules are connected with the genital glands, and are not, as the posterior are, secretory in nature. If the testes were functional at this time—which they are not—the spermatozoa and urine of the Wolffian body would pass to the cloaca by the Wolffian duct.

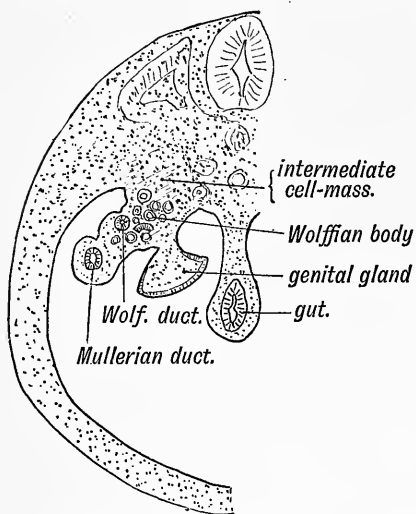


FIG. 384.—Diagrammatic Section to show the Position of the Wolffian and Genital Ridges on the Dorsal Wall of the Abdomen.

Origin of the Wolffian Duct and Tubules.—The tubules which compose the Wolffian body are developed in the **intermediate cell mass**, in the manner already described

(p. 359). The intermediate cell mass is divided from before backwards into segments; two or three tubules arise in each segment. The tubules, although of the nature depicted in Fig. 380, appear in the course of human development as minute vesicles in the intermediate cell mass; these vesicles become tubular; one end opens into the Wolffian duct; at the other a glomerulus is developed (see Fig. 381). The duct is developed in the outer part of the intermediate cell mass. Its anterior or cervical part appears early in the 4th week as a solid rod of cells formed by the union of the terminal ends of the pronephric tubules. By the end of the 4th week the caudal end of the pronephric duct has reached the cloaca and thus the pronephric duct forms the basis of the Wolffian duct—the duct into which the tubules of the Wolffian body open. At first the hinder or pelvic ends of the Wolffian bodies are separate, but in the 8th week they become approximated and fuse to form the **genital cord**. The genital cord contains the terminal parts of the Wolffian and Müllerian ducts. The Müllerian ducts being situated nearest to the middle line, fuse to form the uterus.

The Pronephros.—Pronephric differ from mesonephric tubules in retaining open peritoneal funnels attached to them (Fig. 383) and in having their glomeruli occasionally situated within the peritoneal cavity (Fig. 381). They reach their highest development in anterior segments of the human embryo during the 4th week and then disappear, leaving no trace. Their duct becomes the Wolffian duct, and if a remnant did persist we should seek for it at the commencement of this duct.

The Fate of the Wolffian Body (mesonephros) and Pronephros.—
1. In the **Female.**

In Fig. 385 are shown the various remnants of the embryonic renal formations which may persist in the adult female. The Müllerian duct, the upper part of which becomes the Fallopian tube, is situated in the

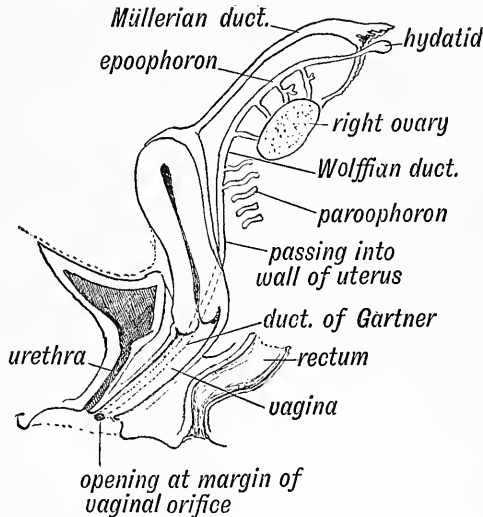


FIG. 385.—Remnants of the Wolffian Body in the Female (see also Fig. 387).

Wolffian ridge (Fig. 384). Hence when the ovary and tube migrate to the pelvis, the Wolffian mesentery, which comes to form the mesosalpinx, is also drawn within the pelvis, and with it all the Wolffian remnants. A hydatid attached to the mesosalpinx (part of the broad ligament) at the fimbriated extremity of the Fallopian tube (Fig. 385) represents the most anterior (cephalic) part of the Wolffian formation. The Wolffian duct (Fig. 385) runs towards the body of the uterus in the mesosalpinx; it reaches the side of the uterus, but from that point onwards it has disappeared by the commencement of the 3rd month. Occasionally, however, remnants of the lower or distal part of the duct persist. They lie in the roof of the vagina. The point of termination of the duct is sometimes represented on the trigone of the vulval cleft a little distance from the side of the opening of the urethra. Only the upper part of the duct (mesosalpingeal part) persists in women. The uterine and vaginal segments, when they persist, get the name of **duct of Gartner**. The **genital tubules**, those attached to or connected with the ovary, persist and form the

epoophoron, Organ of Rosenmüller, or parovarium. The **renal Wolffian tubules**—those which acted as renal structures in the embryo—also persist, sometimes unconnected with the duct. They lie between the ovary and uterus and form the **paroophoron**. Fluid may collect in their cavities, and thus those vestiges may form cysts, but, as we shall see (p. 366), the Wolffian remnants which are the usual source of cystic formations in the female lie along the ovarian fimbria and are derived from the elements which give rise to the rete testis in the male.

2. In the Male.

In the male (Fig. 386) the Wolffian duct forms :

(1) The tube of the epididymis, which is coiled up in the globus major, body and globus minor of the epididymis ;¹

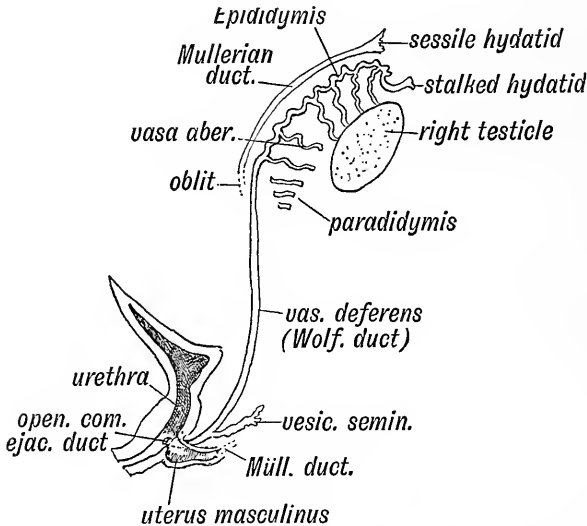


FIG. 386.—Remnant of the Wolffian Body in the Male (see also Fig. 387).

(2) The vas deferens and common ejaculatory duct. The duct opens at each side of the uterus masculinus in the prostatic urethra, a site corresponding to the vestibule of the vagina in the female ;

(3) The vesiculae seminales arise from the Wolffian ducts as tubular diverticula at the end of the 3rd month ; the terminal part of the duct also becomes dilated to form an ampulla.

The stalked hydatid frequently seen on the upper extremity of the testicle corresponds to the hydatid at the fimbriated extremity of the Fallopian tube in the female, and is of similar origin (Figs. 385 and 386).

The **genital tubules** of the Wolffian body become the vasa efferentia and coni vasculosi.

¹ J. L. Bremer, *Amer. Journ. Anat.* 1911, vol. 11, p. 393 (Dev. of Vasa Efferentia); Otto Petersen, *Anat. Hefte*, 1907, vol. 34, p. 239 (Dev. of Vesiculae Seminales); E. M. Watson, *Amer. Journ. Anat.* 1918, vol. 24, p. 395.

The **renal tubules** of the Wolffian body form :

- (1) The vasa aberrantia found in the globus minor ;
- (2) The paradidymis or organ of Giraldés situated in the cord above the globus major but not always present. The vas aberrans represents an elongated Wolffian tubule, which has effected a communication with the Wolffian duct, but not with the genital gland. The tubules of the paradidymis represent blind tubules, which retain the embryonic cystic form. All these tubules, both genital and renal of the Wolffian body, are situated originally in the mesentery of the Wolffian body (Fig. 384).

Thus it will be seen that while in the male the Wolffian tubules and duct become part of the genital system, in the female they become functionless and only of pathological importance. Their presence in the female is due

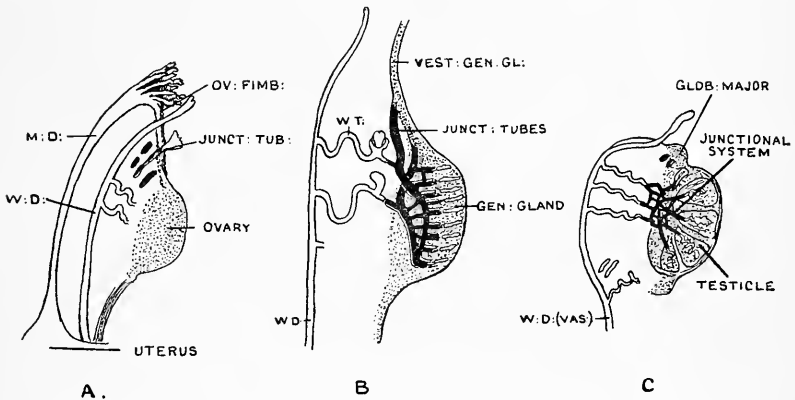


FIG. 387.—Diagrams showing the fate of the Junctional Cords in the Ovary and in the Testis. *A*, ovary and Fallopian tube, showing the rudiments of the junctional tubules in the ovario-fimbriate margin of the broad ligament; *B*, the origin of the junctional system; *C*, the junctional system of the testis. *M.D.* Müllerian duct; *W.D.* Wolffian duct; *W.T.* Wolffian tubules.

to their being inherited from the male, just as the breasts in the male persist because of their utility in the female.

Rete Testis.—The junction between the genital tubules of the Wolffian body and the seminal tubules of the testes is effected by the development of a separate element to which the names of rete-cords or junctional cords have been given. In Fig. 387, *B*, is represented the origin of the junctional tubules, according to the account given by Dr. Allen.¹ The ovary and testis represent only the middle part of the original genital ridge; the anterior and posterior parts atrophy and disappear by the end of the 2nd month. In the anterior vestigial part of the ridge solid cords representing peritoneal funnels (Fig. 380), grow into the mesentery of the Wolffian body, and from these cords, as shown in Fig. 387, *B* (where only two cords are represented), is formed the rete testis. The rete testis effects communications with the seminal tubules by means of outgrowths, which form the vasa recti, and also with the glomerular or blind extremities of the genital tubules of the Wolffian body (Fig. 387, *C*). In the female the

¹ See Bennet M. Allen, *Amer. Journ. Anat.* 1906, vol. 5, p. 79.

junctional cords are formed; vestiges usually remain. Frequently fimbriated hydatids (peritoneal funnels) are attached to them (Fig. 387, A). The majority of parovarian cysts¹ are formed from the junctional rudiments. Isolated vestiges may also be seen in the testicle between its upper pole and the globus major (Fig. 387, C). They also may give rise to cysts.

THE KIDNEY.

Origin of the Permanent Kidney.²—In Fishes and Amphibians the Wolffian body alone acts as a kidney. In Reptiles, Birds and Mammals the permanent or hind kidney appears, and supplants the Wolffian kidney. Like the Wolffian body the kidney arises by the combination of two elements which are developed separately—a duct or collecting system, and a

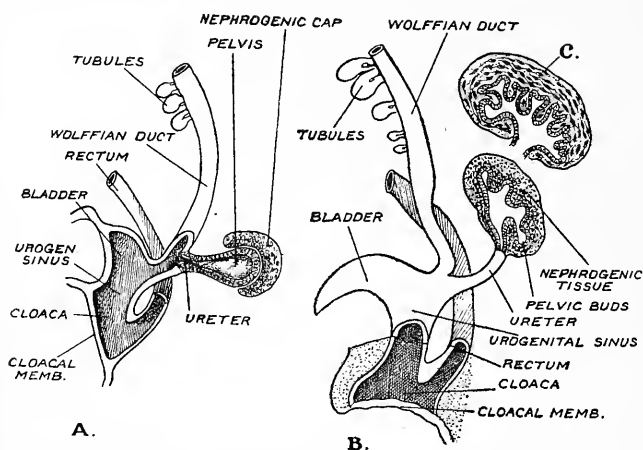


FIG. 388A.—The Ureteric Bud and Nephrogenic Cap at the beginning of the 6th week.
 FIG. 388B.—The same parts later in the 6th week. C indicates the stage of Renal development reached in the 7th week.

nephric or secretory system. The collecting system arises as an outgrowth from the hinder end of the Wolffian duct, and forms the ureter, the pelvis of the ureter and the collecting tubules, which compose the main part of the medullary pyramids of the kidney. The secretory part arises from the hinder end of the nephridial system—just behind the part which gives origin to the mesonephros; it forms the cortex of the kidneys—the glomeruli, convoluted tubules and loops of Henle; in short, the secretory substance of the kidney (Fig. 389). Already, at the beginning of the 5th week, the ureteric part of the kidney is apparent as a dilatation or slight evagination at the hinder end of the Wolffian duct, near the cloaca. The

¹ For the pathological significance of this structure see Alban Doran, *Journ. of Obstetrics and Gynaec. of Brit. Empire*, Oct. 1910, vol. 18, p. 246.

² G. C. Huber, *Amer. Journ. Anat.* 1905, vol. 4, Supplement (Dev. of Renal Tubules); F. T. Lewis, *Amer. Journ. Anat.* 1919, vol. 25, p. 423; A. F. Dixon, *Journ. Anat. and Physiol.* 1911, vol. 45, p. 117 (Supernumerary Kidney); E. Muthmann, *Anat. Hefte*, 1907, vol. 32, p. 577 (Horse-shoe Kidney).

stage reached by the beginning of the 6th week is shown in Fig. 388, *A*; the ureteric bud is stalked, the stalk representing the ureter and its dilated pelvic end the renal pelvis and collecting tubules. The nephrogenic tissue forms a cap on the pelvic dilatation. At this time the kidney lies under the 4th and 5th lumbar segments. At a later stage in the 6th week (Fig. 388, *B*) the ureteric stalk has become elongated, the pelvic dilatation has given rise to primary evaginations representing the calyces of the kidneys; round the evaginations is massed the nephrogenic cap. The kidney now lies dorsal to the Wolffian body and under the 2nd and 3rd lumbar segments.

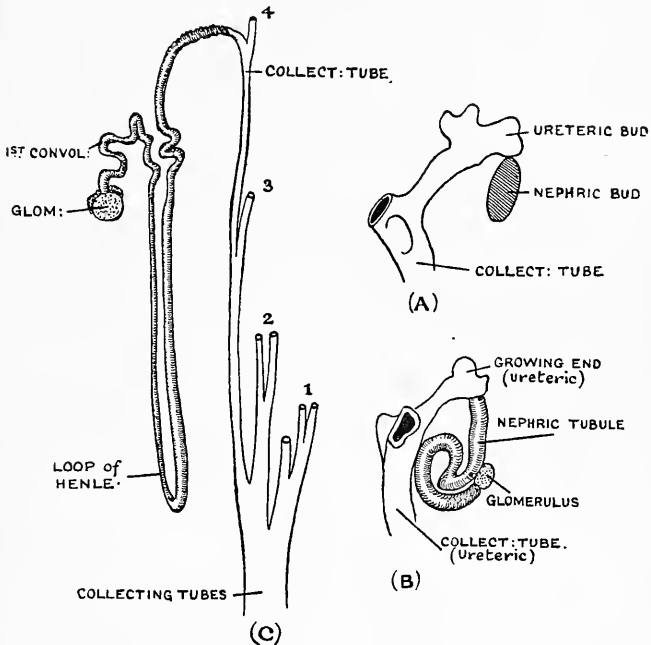


FIG. 389.—Illustrating the Development of the Renal Tissue. *A*, growing end of collecting tubule with bud of nephric tube attached to it; *B*, first stage in the development of a nephric bud into a nephric tubule; *C*, fully developed renal tubule; the part formed from the ureteric bud is represented in outline and the part from the nephric tubule is shaded. (After Huber.)

The separation of the ureter from the Wolffian duct has commenced. In Fig. 388, *C* a still later stage is shown. Tubules now begin to form in the nephrogenic cap and collecting tubules to bud out from the pelvic bud. Collecting tubules arise by the division and redivision of the growing end of the pelvic outgrowths. In the third month the process of outgrowth from the ureteric bud continues; the growing end of each bud divides and redivides, and in this manner the collecting tubules of the pyramids are formed (Fig. 389, *C*). In Fig. 389, *A*, the growing extremity of such a collecting duct is represented. Near one of its terminal buds is represented one of the numerous tubule-rudiments, formed from the nephrogenic tissue surrounding the ureteric outgrowths. Like a Wolffian tubule, it appears in a vesicular form. At one extremity it establishes a communication

with the collecting tubule; at the other a glomerulus develops (Fig. 389, *B*). The tubule elongates, becomes convoluted, and quickly assumes the adult form represented in Fig. 389, *C*. Glomeruli appear at the commencement of the 3rd month; a capsule becomes differentiated for the kidney from the surrounding mesodermal tissue in the 3rd month. The kidneys have by then reached their final position—extending from the 11th thoracic to the 4th lumbar segment. Up to the time of birth, tubular and glomerular formation are seen in full activity within the subcapsular zone of the kidney. The deep tubules are the first to differentiate. Soon after birth the formation of new elements ceases; increase in size is then due to pure growth of the parts already formed. The collecting tubules, arising from each primary evagination of the ureteric bud become massed in pyramids; the bases of the pyramids, clothed by nephrogenic caps, appear on the surface of the kidney and give it a lobulated structure. In the fissures between the lobules cortex is formed; soon after birth, as new cortical tissue is laid down, the depressions between the lobules are filled up. In many mammals (ox, bear, seal) the renal substance remains broken up into numerous lobules.

The upper pole of the kidney reaches the 11th rib in the 5th month, and is then in juxtaposition with the adrenal, which is developed at the anterior end of the Wolffian body. At their first appearance the renal buds receive temporary branches from the common iliac artery and from the aorta, but when they come to lie on the dorsal aspect of the Wolffian body in the 7th week, the arterial network, supplying the tubules of that body, invade the nephrogenic tissue of the renal buds and thus the kidneys annex the series of Wolffian arteries—stretching from the 11th thoracic to the 4th lumbar. The definite arteries are derived from those of the 2nd lumbar segment but frequently more than one pair persists.

With the development of the lumbar and sacral regions of the body the ureter becomes elongated. The termination of the ureter becomes separated from the Wolffian duct early in the 7th week, by a process to be mentioned later.

As the kidney grows forwards its hilum at first looks towards the pubic region, and even when it has reached its final position and the poles become upper and lower, the hilum of the kidney still looks towards the ventral wall of the abdomen. In the 4th and 5th month an anterior lip is formed to the hilum by the development of cortical tissue, and the hilum then assumes its normal form and position. The anterior lip is usually absent from **horseshoe kidneys**, an abnormality which arises from a fusion of the right and left nephrogenic buds. Such kidneys are usually supplied with multiple renal arteries. In other cases the renal buds grow, not towards the loins but towards the sacral region, becoming developed in the pelvis and drawing their arteries from the sacral and iliac vessels. The ureteric bud may divide, and give rise to a forked ureter, or to double or even triple ureters. The nephrogenic element may remain single, or it also may become divided, giving rise to two kidneys on one side. Another common developmental error is the failure of the nephric tubules to effect a union

with the collecting tubules. The nephric tubules then become dilated and cystic, giving rise to **congenital cysts** of the kidney.

THE MÜLLERIAN DUCTS.

The **Müllerian Ducts**¹ or **Oviducts** are present in almost all vertebrates, and convey the ova from the peritoneal cavity to the surface of the body. In fishes, amphibians, reptiles, birds and lower mammals (Marsupials) the ducts terminate in the cloaca. This is also the case in the embryonic stages of man and all higher mammals. The development of the duct in man is very simple (Fig. 390). The first part to be formed is the ostium abdominale which appears on the ventro-lateral aspect of the Wolffian ridge (Fig. 390) as a funnel-like invagination of the coelomic mesothelium. This invagination, which appears in the 6th week at the anterior end of the Wolffian ridge (under the 3rd thoracic segment) represents a modified

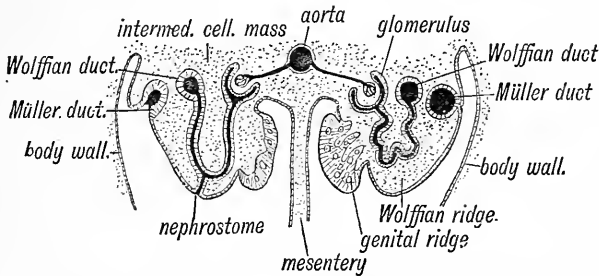


FIG. 390.—Diagrammatic Section across the Wolffian and Genital Ridges to show the Origin and Relations of the Müllerian Duct to the Duct and Tubules of the Wolffian Body. (After Pasteau.)

peritoneal funnel (Fig. 380) or nephrostome (Fig. 390). From the apex of the funnel-like invagination of coelomic epithelium, a solid rod-like process of cells grows backwards on the Wolffian ridge, ventral to the Wolffian duct (Fig. 384) reaching the region of the cloaca in the 7th week. Although the ostium is developed thus, the fimbriae which surround it are not formed until the 3rd month, when they appear as outgrowths of the lining membrane of the tube. More than one ostium may be developed, representing neighbouring nephric funnels. As it passes backwards in the Wolffian ridge the Müllerian duct lies below and internal to the Wolffian duct and comes in contact with its neighbour of the opposite side in the pelvis (Fig. 392). The Müllerian duct is formed in the embryo later than the Wolffian duct; its posterior growing end does not acquire a lumen until late in the 3rd month when it opens on the dorsal wall of the urogenital sinus—a derivative of the cloaca (Fig. 391). The openings of the two Müllerian ducts are situated between the orifices of the Wolffian ducts. Müllerian ducts, although they only reach their full development in woman, are yet as completely and strongly formed in the male embryo as in the female.

¹ S. E. Wichmann, *Anat. Hefte*, 1912, vol. 45, p. 629.

By the beginning of the 3rd month the fimbriated tube has retreated to the level of the 2nd lumbar segment.

The Genital Cord.—During the 3rd month the Müllerian ducts show two distinct stages in their course :

(1) **Lumbar**, which lies in the Wolffian ridge and is suspended from the posterior abdominal wall by the Wolffian mesentery. This stage afterwards forms the Fallopian tube (Fig. 392).

(2) **Pelvic**, which is embedded in the genital cord. The posterior ends of the Wolffian ridges, with their contents, the Wolffian and Müllerian ducts, fuse in the pelvis during the 8th week, and thus form the **genital cord**.

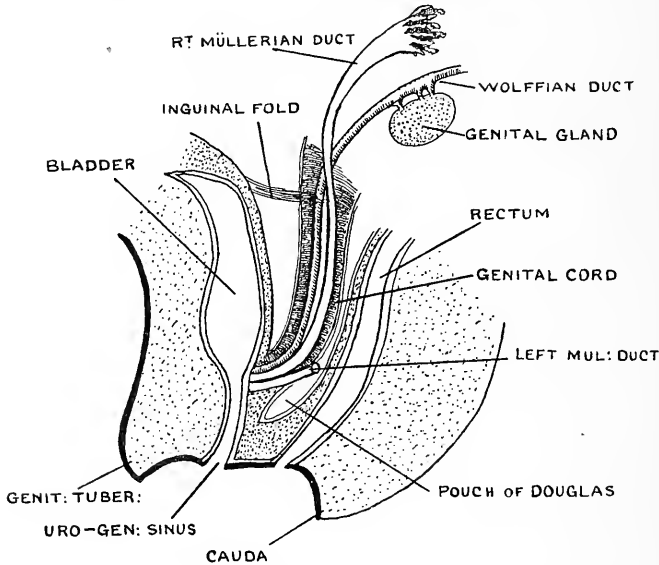


FIG. 391.—Diagram of the Genital Ducts at the commencement of the 3rd month of Foetal Life. Lateral view.

With their fusion the peritoneal space of the pelvis is separated into a deep posterior part—the pouch of Douglas and a shallow anterior depression—the utero-vesical (Fig. 391). The parts of the Müllerian ducts within the cord form the uterus and vagina. The ureter is also enclosed within the mesodermal tissue of the genital cord, but afterwards becomes separated from it.

The genital cord of the foetus at the beginning of the 3rd month shows the two Müllerian and two Wolffian ducts—in the male as well as in the female (Fig. 391). One of the first signs of sexual differentiation is to be observed in the genital cord. Whereas the genital cord in the male embryo is closely applied to the bladder, so that there is no utero-vesical pouch, in the female the cord remains separated from the bladder by a deep peritoneal pocket.

The Round Ligament of the Uterus, which is apparent early in the 3rd month, is attached to the Müllerian duct on each side (Fig. 392). The

point of attachment marks the junction of the uterine and Fallopian segments of the Müllerian ducts. The round ligament corresponds to the **gubernaculum testis** in the male and its development is similar. Both are developed in the following manner :

Part of the Wolffian ridge is continued backwards as a peritoneal fold to the groin, this part forming the **inguinal fold** (Fig. 392). Within the inguinal fold, in the mesenteries of the Wolffian body and genital gland and in the subperitoneal tissue of the genital cord a stratum of non-striated muscular tissue is developed. The mesodermal tissue, in the lower end of the inguinal fold, begins to pierce the abdominal wall external to the deep epigastric artery in the 3rd month, the piercing force being obtained purely from the inertia of growth. The growing end, at first merely

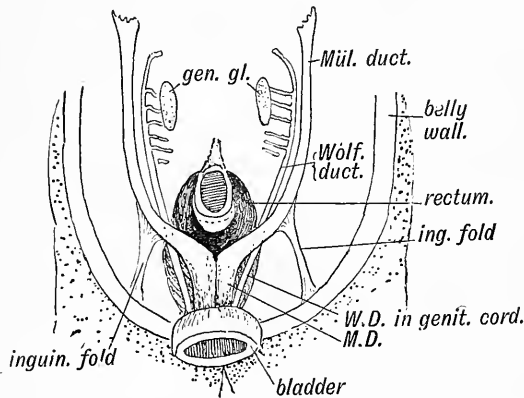


FIG. 392.—Diagram of the Müllerian Ducts at the commencement of the 3rd month.
Ventral view.

represented by fine strands of tissue, in later months increases in mass, and carries over it and in front of it, into the scrotum or labium majus, a process of the peritoneum and attenuated representatives of each stratum of the belly wall (Fig. 421). The inguinal canal, the round ligament of the uterus and the gubernaculum testis are thus formed by the extension of the substance of the inguinal fold. From the stratum of muscular tissue which is found everywhere under the pelvic peritoneum, particularly around the genital cord, are formed the round ligament of the ovary, the muscular tissue in the utero-rectal (utero-sacral) ligaments and in the broad ligaments, and also the outer muscular coat of the uterus.

Formation of Uterus and Vagina.—The parts of the Müllerian ducts lying side by side in the genital cord (Fig. 392) begin to unite in the 3rd month, and by their fusion the uterus and vagina are formed. In all the members of the vertebrate series below and including the Monotremes, the Müllerian ducts remain separate and open in the cloaca (Fig. 393, *A*). The process of fusion begins with the formation of the genital cord in the 8th week and is continued throughout the 3rd month. The septum formed by the fused mesial walls (Fig. 394) disappears first below the region of

the uterine cervix; the process may be arrested at this stage—a stage shown by some adult marsupials. Next, the lower or cervical part of the uterine septum disappears; the human uterus then ($2\frac{1}{2}$ months) resembles that of higher mammals (carnivora, etc., Fig. 393, *C*). It may be arrested at this stage (uterus bicornis). Lastly the upper part of the septum disappears ($3\frac{1}{2}$ months, Fig. 394). The fundus, which is the last part to be developed and is only found in the highest primates, is quite well marked in the child at birth.

The musculature¹ appears in the wall of the uterus, vagina and tubes during the 4th month, the inner or circular layer appearing before the

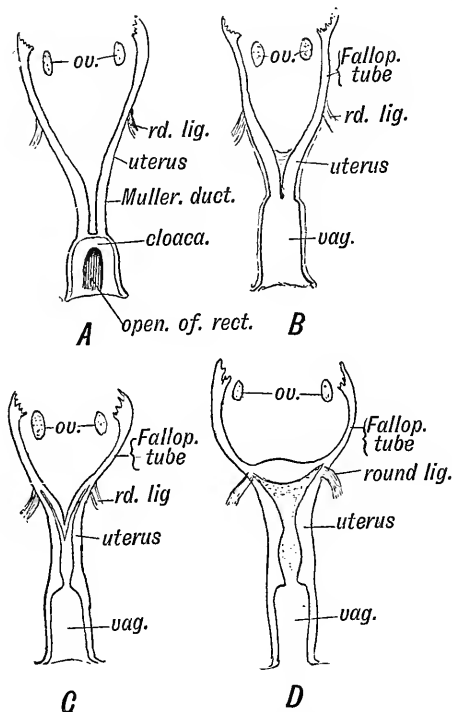


FIG. 393.—Evolution of the Human Form of Uterus.

A, form seen in lowest mammals, reptiles, amphibians, fishes, and in the 2nd month human foetus; B, form of Müllerian ducts in rodents; C, form in carnivora, etc., and in the 3rd month human foetus; D, form found in man and higher primates.

outer or longitudinal. Sometime after birth additions are made to the musculature of the uterus, and the distinction between the two primary layers becomes obliterated. Glands begin to form in the uterine mucosa during the 4th month and at the same date the cervix becomes differentiated from the vagina. At this time, too, the ovarian extremity of the Fallopian tube becomes wide and trumpet-shaped; the mucous membrane within it becomes plicated. The fimbriae are then formed by the extremities

¹ H. R. Clarke, *Journ. Obstet. Gynae.* 1911, vol. 20, p. 85.

of the plicae growing out at the ostium abdominale. Secondary or accessory ostia may also be produced.

By the 7th month (Fig. 402) the foetal uterus is divided into two parts, the cervix or lower segment and body or upper segment. The lower segment or cervix forms then two-thirds of the uterus; its walls are thick and its upper part is lined by columnar non-ciliated epithelium, containing racemose mucous glands. Its mucous membrane is arranged in palmate folds. The upper or uterine segment composes only a third of the uterus. It is lined by columnar epithelium, which becomes ciliated at the end of foetal life. At puberty the body of the uterus, instead of being half the size of the foetal cervix, becomes larger than it. The cervix takes no

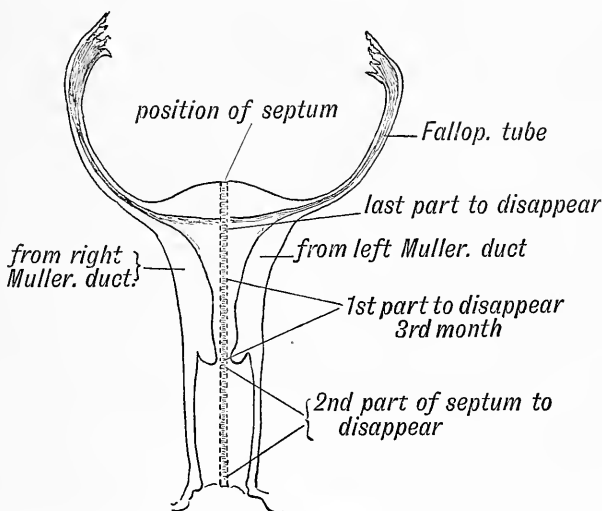


FIG. 394.—Showing the manner in which the Müllerian Ducts fuse to form the Uterus and Vagina.

part in menstruation nor in containing the foetus; its true function is unknown. The external os is formed at the junction of the vaginal cords with the uterine segment of the Müllerian ducts; it becomes demarcated at the end of the 4th month. For some time after birth the body of the uterus actually undergoes a reduction in size (Bayer); growth does not become marked until the 7th year.

Metamorphosis of the Vagina.—About the middle of the 3rd month the lower ends of the Müllerian ducts of the human embryo undergo a remarkable metamorphosis, first fully described by Berry Hart and lately reinvestigated by F. Wood Jones.¹ The epithelium lining the vaginal tracts of the Müllerian ducts proliferates, forming two cords of cells, while, at the same time, the mesodermal tissue in the lower end of the genital cord, which surrounds the terminal segments of the Müllerian and Wolffian ducts, undergoes a rapid growth, pushing downwards that part of the cloaca in which they end—the urogenital sinus (Fig. 395, I., II.). The vaginal

¹ *Brit. Med. Journ.* 1904, Dec, 17th; *Journ. Anat.* 1914, vol. 48, p. 268.

cords formed by the Müllerian linings (Fig. 396) proliferate into the tissue of the genital cord and fuse together, the vagina being formed by the breaking down of the epithelial core in the 4th month. Thus the orifice of the

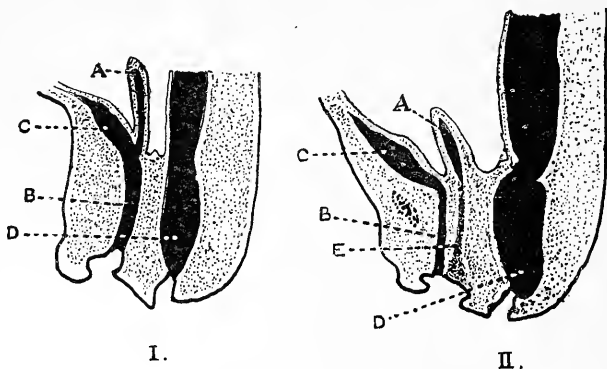


FIG. 395.—Diagrams showing the Termination of [the] Vagina about the seventh week (I.) and about the thirteenth week (II.). (After Wood Jones.) A, Müllerian ducts (vagina and uterus); B, urogenital sinus; C, bladder; D, rectum; E, vagina represented by a cord of epithelium.

vagina, originally situated high in the urogenital sinus, is carried downwards until it opens in the vulval cleft. **Atresia** of the vagina results from a failure of the process of canaliculization. Septa in the vagina result from incomplete fusion of the two cords. Only the tip of the vaginal cords

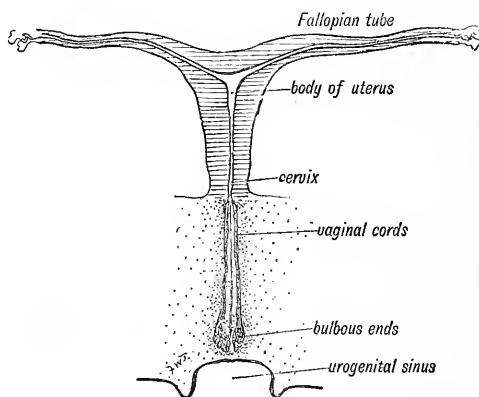


FIG. 396.—Diagram illustrating the manner in which the Vagina is formed by the Fusion of two solid Processes or Cords. (Wood Jones.)

reach the urogenital sinus; hence a partial septum—the **hymen**¹—marks the opening of the vagina into the urogenital sinus. The extent to which the terminal septum breaks down varies widely; hence the numerous forms assumed by the hymen.

¹ For development of hymen: D. Berry Hart, *Edin. Med. Journ.* 1911, vol. 6, p. 577; F. J. Taussig, *Amer. Journ. Anat.* 1908, vol. 8, p. 89.

An explanation of this remarkable change may be found in the formation of a new vagina in lower marsupials which was discovered by J. P. Hill.¹ In lower marsupials the vaginal segment of the Müllerian ducts are separable into two parts—upper, which lie side by side, and reach towards the cloaca (Fig. 397); lower, which form lateral loops before terminating in the cloaca. Hill found that the young were born by passing from the upper or median segments into the cloaca by the formation of a new passage (Fig. 397). In higher marsupials he found that the upper parts of the vaginal segments became fused to form a median vagina, and that the new passage to the cloaca was not temporary as in lower marsupials, but permanent. In monotremes, the Müllerian ducts have to serve only for the passage of unhatched ova, but with the evolution of gestation the

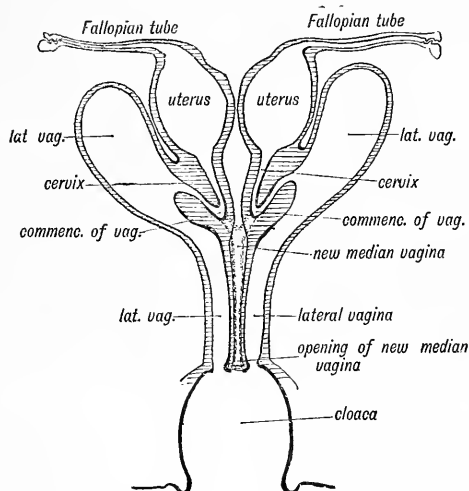


FIG. 397.—Diagram showing the arrangement of the Müllerian Duct in a Marsupial Mammal and the manner in which a New Vagina is formed for the Passage of the Young at Birth. (F. Wood Jones after J. P. Hill.)

ducts, which could convey ova, were unfitted for the transmission of young, and a new passage or median vagina was formed. The evidence is conclusive that there was a phase in human evolution when the Müllerian ducts terminated in a cloaca, and the metamorphosis which takes place in the lower ends of these ducts of the human embryo is evidently an abbreviated recapitulation of the formation of the median vagina of marsupials.

The Müllerian Ducts in the Male.—In the male foetus of the 3rd month the Müllerian ducts are undergoing atrophy, the distinction between the testis and ovary being quite marked by that time, and the process of sexual differentiation already to be seen on close examination. All that remain of the Müllerian ducts in the adult male are their fused terminal

¹ *Proc. Linnean Soc. New South Wales*, 1899, March 29th, p. 42; 1900, Aug. 29th, p. 519.

or vaginal segments forming the sinus pocularis or uterus masculinus in the prostate (Figs. 386, 398). Its depth is commonly about 3 or 4 mm., but occasionally such a form as is represented in Fig. 399 occurs and shows the real nature of the sinus pocularis. The vagina and uterus can be recognized in such cases (Primrose). The fimbriated ends of the Müllerian ducts persist as the sessile hydatids on the testicle (Fig. 386). The intermediate part of the tube disappears in the 3rd month and its site becomes

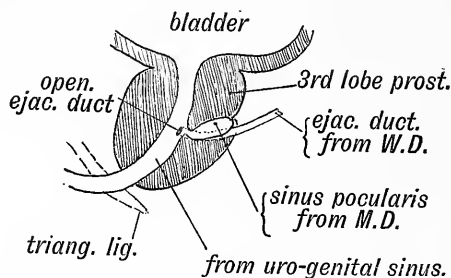


FIG. 398.—A Section of the Prostate showing the Remnants of the Lower Ends of the Müllerian Ducts in the Male.

greatly stretched during the descent of the testicle. A remnant of its upper end can be found in the sharp anterior border of the epididymis until quite a late period in foetal life.¹ The mesosalpinx shrinks and completely disappears in the anterior border of the epididymis.

The Urogenital Sinus or Canal.—The Müllerian ducts open into the cloaca of the embryo side by side, between and below the openings of the Wolffian ducts (Fig. 391). The passage which serves as a common channel

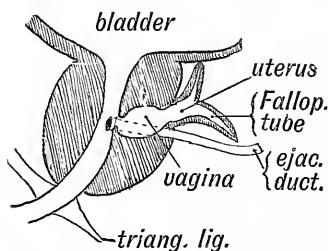


FIG. 399.—A Section of a Prostate showing an unusually developed Uterus Masculinus. (After Primrose.)

for bladder, Müllerian and Wolffian ducts is the urogenital sinus (Fig. 400, *A*, *B*). In the female foetus at the 3rd month it is still well marked. In all mammals except man this passage-like sinus is retained. By the beginning of the 4th month in the female foetus (Fig. 400, *B*) it will be seen that the urogenital sinus has become shortened and opened out to form the floor of the pudendal or vulval cleft from the glans clitoridis in front to the fossa navicularis behind, and thus the end of the Müllerian

¹ J. H. Watson, *Journal of Anat.*, 1902, vol. 36, p. 147.

ducts (vagina) and urethra come to have separate openings. The metamorphosis in the genital cord which leads to the formation of the vagina plays a large part in the transformation (Fig. 395). In the male (Fig. 401) the early foetal form is retained, and the urogenital sinus becomes that part of the urethra between the sinus pocularis and the fossa navicularis

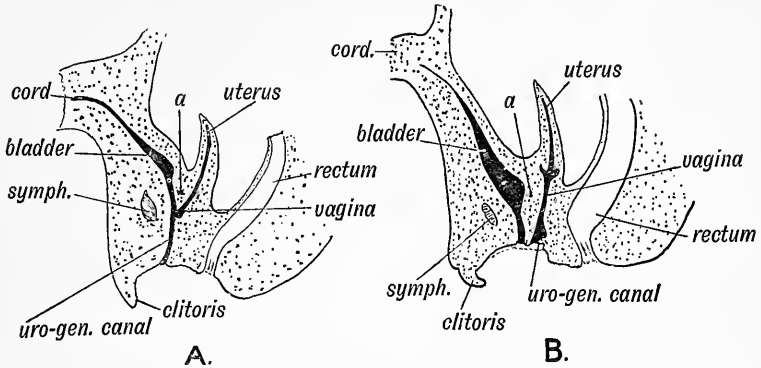


FIG. 400.—Section showing the Urogenital Sinus.

A, in the 3rd month female human foetus ; B, in the 5th month female human foetus ; a, the vesico-vaginal septum.

in the glans penis. The female urethra corresponds to the prostatic part above the opening of the sinus pocularis of the male urethra (Figs. 400, 401).

The Hymen¹ is formed at the junction of the vagina with the urogenital sinus, being covered on its outer surface by epithelium derived from

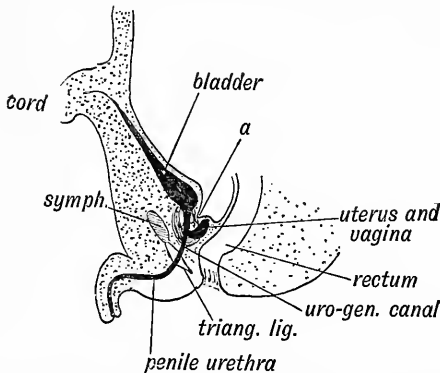


FIG. 401.—Section showing the Urogenital Sinus in the Male Foetus.

a indicates the part corresponding to the vesico-vaginal septum of the female. It is occupied by the 3rd lobe of the prostate.

the urogenital sinus, and on its deep surface by epithelium of the vaginal cord. Usually at one point on the hymen, but occasionally at several,

¹ See references, p. 374.

the epithelial coverings fuse and break down, leading to one or more perforations. On the other hand, the vaginal cords may not reach the urogenital sinus, the hymen being then imperforate. In reptiles, as in

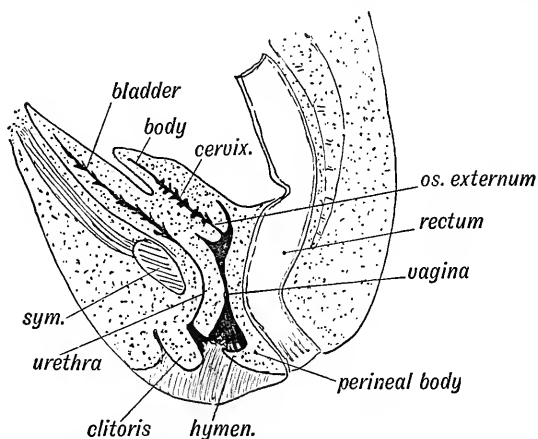


FIG. 402.—A Section to show the condition of the Vagina and Uterus at the 7th month of Foetal Life.

the human embryo, the part of the urogenital sinus into which the Müllerian and Wolffian ducts open, forms the trigone of the bladder (see p. 381). In such animals the hymen prevents the reflux of urine into the Müllerian ducts.

CHAPTER XXIV.

UROGENITAL SYSTEM (*Continued*).

Evolution of the Penis.¹—The transformation of the mesonephros to form an adjunct of the genital system of the male is of ancient origin, but those remarkable changes which are seen to occur in the perineum of the human embryo represent a much later evolutionary movement. Even in the lowest mammals—monotremes and marsupials—the rectum and urogenital ducts end in a common terminal passage—the cloaca (Fig. 403, *B*). In the human embryo, until the 7th week of development, this is also the case; but about the beginning of this week, when the embryo is 12 mm. long, changes occur which separate the rectal and urinary passages. These changes have been occasioned by the evolution of an external or extra-cloacal penis. In Fig. 403 stages in the evolution of the penis are represented. In the tortoise the penis lies on the pubic or ventral wall of the cloaca; during copulation the cloaca is partially everted and the open groove of the penis is converted into a canal by the application of the dorsal or opposite wall of the cloaca. In *Echidna*—a primitive mammal—the penis is still intra-cloacal; its groove is converted into a canal, except posteriorly, where there is still a communication between the urogenital and cloacal passages—which represents the primitive urogenital orifice, for the penile canal is a new passage (Fig. 403, *B*, 4). In marsupials (Fig. 403, *C*) the penis is still partially intra-cloacal, but the primitive urogenital orifice is closed, and the urogenital passage is now separated from that which serves for the faeces. In man the penis, as in all primates, has been permanently extruded and is now completely extra-cloacal, and a perineal body separates the rectal orifice from the urogenital passage. The **metamorphosis of the cloaca** is thus a result of the evolution of the penis. The external penis with a complete penile urethra appears with the evolution of a vagina, uterus and the intra-uterine nourishment of the young. The cloacal passage is seen in oviparous mammals; in viviparous mammals the penis is evolved as an intromittent organ, and the urogenital passage is separated from that of the rectum.

Twofold Origin of the Cloaca.—The primitive cloaca, as represented in Fig. 403, *A*, is of double origin, the deeper part in which the rectum and urogenital sinus end is derived from the hind-gut and is thus of entodermal

¹ See articles by Prof. Wood Jones, *Journ. Anat.* 1914, vol. 48, p. 73; 1915, vol. 49, p. 393; 1916, vol. 50, pp. 1, 189.

origin. The more superficial part, enclosed by the cloacal lips, arises as a perineal depression and is thus of ectodermal origin. Students of embryology, however, when they speak of cloaca, have in mind only the part derived from the hind-gut—the entodermal cloaca. The development of the perineal region cannot be understood unless it is remembered that both ectodermal and endodermal elements play a part in fashioning the anal and vulval orifices of the human embryo.

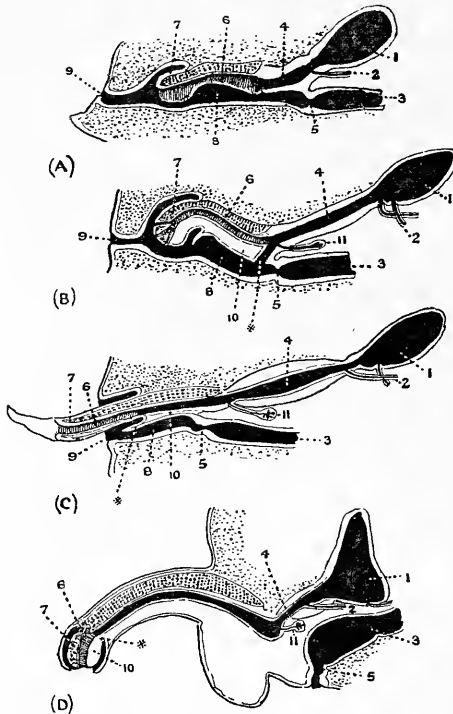


FIG. 403.—Stages in the Evolution of the Penis. *A*, stage seen in tortoise; *B*, stage seen in Echidna; *C*, stage seen in marsupial (kangaroo); *D*, stage seen in man. 1, bladder; 2, Wolffian duct (vas); 3, rectum; 4, urogenital sinus; 5, anus; 6, phallic groove and canal; 7, glans; 8, cloaca; 9, cloacal orifice; 10, floor of phallic canal; 11, Cowper's glands; * position of primitive orifice of urogenital sinus.

The Cloaca of the Embryo.¹—Having in the previous chapter traced the origin and fate of the genital ducts, it is now necessary to follow the changes which are undergone by the cloaca—the common vent for the rectum and genital passages. We have already seen that the cloaca appears early in the 4th week (Fig. 274); its precocious origin being undoubtedly due to the fact that it gives origin to the allantois, by means of which the chorionic circulation is established. Thus in the 4th week (Fig. 407, *A*) the cloaca forms a relatively large cavity, into which open the rectum and allantois, while the Wolffian duct is also establishing a communication

¹ A. G. Pohlman, *Amer. Journ. Anat.*, 1911, vol. 12, p. 1 (Dev. of Cloaca).

with its more ventral part. At this time the outline of the cloaca, as seen on making a median section of the embryo, is triangular in outline; its dorsal wall follows the curve of the notochord to the point of the tail; a large part of its ventral wall is formed by the cloacal membrane—which is composed of only the two primitive layers—the entoderm which lines the cloaca, and the ectoderm which covers the embryo. It will be remembered (see p. 35) that the hinder end of the embryonic body is produced on each side of the primitive streak. The cloacal membrane occupies the site of a part of the primitive streak, thrust into a ventral position by the outgrowth of the tail (Fig. 404). The hinder apex of the cloaca extends beneath the tail and behind the cloacal membrane and forms that transitory structure known as the **tail gut**. In the 4th week the cloaca has no perineal

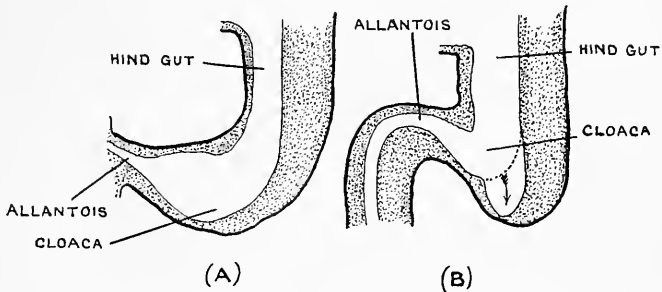


FIG. 404.—The Formation of the Cloaca from the Hind-gut during the 4th week. (Wood Jones.) *A*, section of the posterior end of a human embryo early in the 4th week; *B*, later in the 4th week when the hind fold is more produced and the cloaca assuming its triangular form.

opening; that opening is first established near the end of the 2nd month by an absorption of the cloacal membrane.

Evolution of Cloacal Structures.—To understand the significance of the changes undergone by the cloaca in the human embryo, one must have first a clear conception of the various evolutionary stages known to the comparative anatomist. We have already seen that some of these changes are related to the differentiation of an external penis; it is now necessary to see how the cloaca becomes modified to assume its mammalian and human form. The essential stages are represented in Fig. 405; in the frog (*A*) the cloaca receives the bladder, rectum and Wolffian duct, the duct opening distal to the rectum, being thus nearer the cloacal vent. In the tortoise (*B*) the rectum has passed distal to the Wolffian duct, which now opens with the bladder into a common part of the cloaca—the **urogenital sinus** (Fig. 405, *B*, *UG*). In the lowest mammals—monotremes (*C*)—the urogenital sinus has become elongated and assumed the form of a urethra; the ureter is now severed from the Wolffian duct, but still opens on the floor of the urogenital sinus; the urine thus has to pass across the urogenital sinus to reach the bladder. In marsupials (*D*) a further stage is reached; the cloacal anus of the rectum has migrated backwards on the posterior wall of the cloaca until it almost reaches the perineum. This posterior migration of the rectal opening (anus) is already seen in

Echidna (*C*), where the urogenital sinus—which represents the proximal part of the cloaca—has assumed a considerable length. Thus in the evolution of mammals we see that the rectum migrates backwards until its vent or anus almost reaches the surface of the perineum, leaving the greater part of the cloaca as the urogenital sinus.

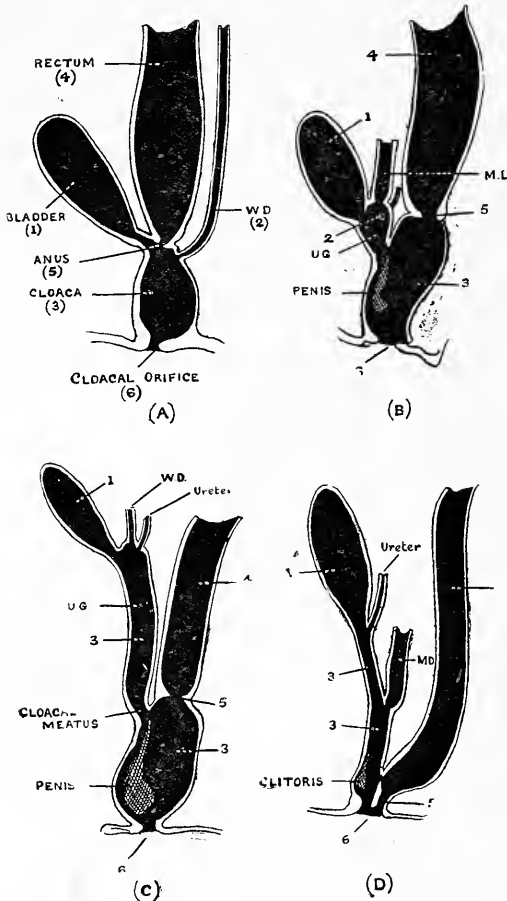


FIG. 405.—Diagrams to show the manner in which the Cloaca is modified and the Termination of the Rectum transferred from the Cloaca to the Perineum in Higher Vertebrates. *A*, the amphibian form; 1, bladder; 2, Wolffian duct (ureter and vas); 3, cloaca; 4, rectum; 5, intra-cloacal anus; 6, cloacal orifice; *M.D.*, Müllerian duct; *B*, form found in the tortoise; *C*, form in monotremes; *D*, form found in female marsupial; *X*, floor of urethra.

Ectodermal Cloaca.—The forms of cloaca depicted in Fig. 405 are not entirely derived from the gut or entodermal cloaca, which is seen in the human embryo. The terminal or superficial part is derived from a **cloacal depression** or pit formed on the perineum, and lined by epithelium derived from the ectoderm. The glans of the penis and also of the clitoris are formed in the ectodermal part: the rest of the penis and clitoris is

developed in the entodermal part (Fig. 403). We have already seen how the urethral groove of the cloacal penis becomes closed off as a separate channel by the union of two vestibular folds—**seminal guides** Prof. Wood Jones has named them—the penile urethra being thus enclosed. In *Echidna* (Fig. 403, *B*) one sees that the urethra is made up of two parts—an upper derived from the urogenital sinus, and a lower or penile from the channel enclosed by the lateral vestibular folds. At the junction of these two parts of the urethra there is still an orifice forming a communication between the urogenital sinus and the cloaca and representing the primitive opening of the urogenital sinus (Fig. 403, *B*). In marsupials the primary urethra (urogenital sinus) and secondary or penile urethra have united by the closure of the primitive opening of the urogenital sinus, and thus the passage for the urine and semen become completely separated

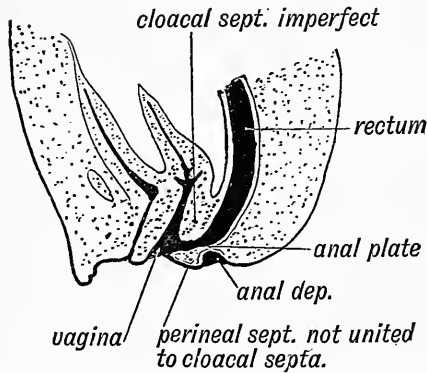


FIG. 406.—Case of a Female Child in which the Rectum opened on the Vestibule while the Normal Anus remains closed by the Anal Plate. The opening on the vestibule represents the ancient cloacal orifice of the rectum.

from the passage for the faeces. The rectum is detached from the urogenital sinus and opens directly into the ectodermal cloaca.

Differentiation of the Human Cloaca.—We are now in a position to interpret the changes which occur in the human cloaca during the 5th, 6th and 7th weeks of development (Fig. 407). In the 5th week the rectum ends proximal to the Wolffian duct as in the frog; in the 6th week the cloacal orifice of the rectum has moved backwards, leaving the proximal part of the cloaca as the urogenital sinus, a condition similar to that seen in *Echidna* (Fig. 405, *C*). As in that animal, the Wolffian ducts and ureters open close together in the sinus. The appearance presented by the backward migration of the rectal orifice is exactly the same as if the cloaca had been divided into rectal and urogenital cavities by the septum marked "A" in Fig. 407, *B, C*. It is convenient to apply the term given by Retterer to this septal formation—the **urorectal septum**. In the 7th week (Fig. 407, *C*) the orifice (cloacal anus) of the rectum reaches the cloacal depression (ectodermal cloaca) and thus become separate from the urogenital sinus—which now represents practically the whole of the entodermal cloaca. During the 6th week the ventral or pubic part of the

entodermal cloaca is extended forwards to provide the lining of the penile urethra. It represents a direct extension of the urogenital sinus carried within the outgrowing genital eminence (Fig. 407, *C*). The cloacal membrane on the floor of this penile extension of the cloaca breaks down towards the end of the 7th week and the urogenital sinus thus presents a fissure-like opening on the perineum. This fissure corresponds to the groove on the open urethra of the tortoise (Fig. 403, *A*). On each side of the

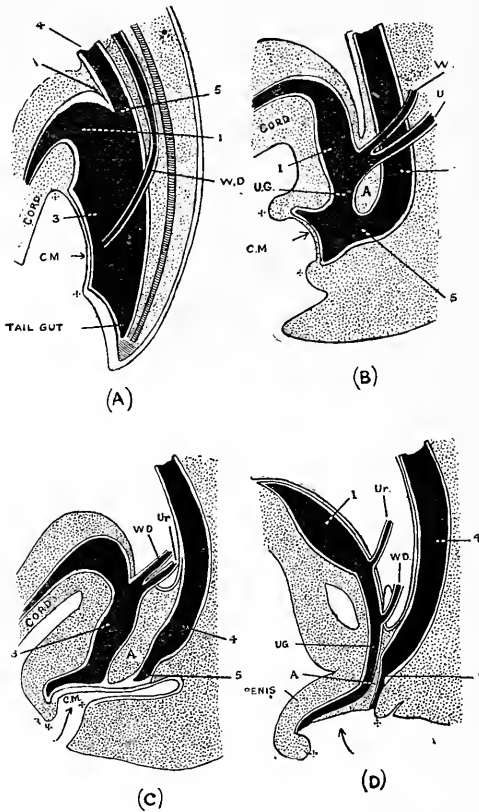


FIG. 407.—Showing the manner in which the Rectum becomes separated from the Urogenital Sinus (entodermal cloaca) during development of the Human Embryo. *A*, Human embryo of 5th week, 4 mm. long; after Keibel. *B*, From human embryo of 6th week, 11 mm. long; after Keibel. *C* and *D*, Later stages of development; 1, bladder; 2, Wolffian duct (ureter and vas); 3, entodermal cloaca; 4, rectum; 5, anus; *C.M.*, cloacal membrane; *U.G.*, urogenital sinus; *A*, Urorectal septum; *B*, penis; **, the limits of the perineal depression (ectodermal cloaca).

perineal fissure, towards the end of the 7th week there appears a fold—the vestibular fold or seminal guide. The hinder ends of the vestibular folds are continuous with the urorectal septum; they unite together in the middle line, union commencing at the urorectal septum and spreading forwards. Their union closes the ancient cloacal orifice of the rectum, but cases frequently occur in which the closure is imperfect and the ancient

cloacal anus persists (Figs. 406, 408, 409). It will thus be seen that in the human embryo the rectal orifice migrates backwards until it opens in the posterior part of the perineal depression (ectodermal cloaca), leaving the whole of the entodermal cloaca of the embryo as a urogenital passage or urethra. All these changes take place during the latter part of the 2nd month.

Malformations of the Rectum and Anus.—When the rectum reaches the perineal depression, it is in contact with and closed by the cloacal membrane (Fig. 407, *C*). The union of the urorectal septum with the hinder ends of the vestibular folds gives rise to the perineal body which separates the anus from the vestibular cleft. The posterior part of the cloacal membrane proliferates, and forms the anal plug. The plug breaks down at the commencement of the 8th week, and the permanent anus is

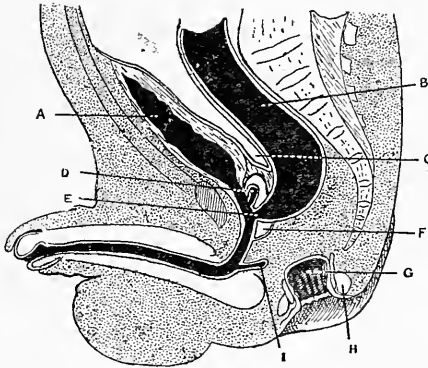


FIG. 408.—Section of Pelvis of a Male Child, showing the Rectum ending in the Prostatic Part of the Urethra. *A*, bladder; *B*, rectum; *C*, recto-vesical pouch; *D*, uterus masculinus; *E*, intra-cloacal anus; *F*, prostate; *G*, anal depression (ectodermal); *H*, external and internal sphincters; *I*, Cowper's gland.

thus formed. This process may fail, giving rise to the condition known as **atresia ani** or imperforate anus. A common degree of malformation is shown in Fig. 408. The migration of the rectum has failed; it opens into the urethra by the ancient cloacal anus and a thick stratum of mesodermal tissue separates the rectum from the anal depression formed by the ectodermal plug derived from the hinder end of the ectodermal cloaca. In Fig. 409 an exactly similar condition is represented in a female infant. The rectum opens in the male below the orifice of the uterus masculinus, in the female at a corresponding point below the orifice of the vagina. The urorectal septum and vestibular folds in the female form merely the perineal body, which separates the terminal part of the rectum from the vulva; in the male they form the floor of the urethra and perineum from the sinus pocularis to the lacuna magna in the glans penis. The terminal part of the male urethra, as we shall see presently, has a separate origin. The downward migration of the vaginal orifice in women brings the cloacal opening of the rectum into the vulva—the floor of the vulval cleft being a derivative of the urogenital sinus. In many cases of imperforate anus

(Fig. 410) the cloacal anus is closed, and the rectum terminates an inch or more from the anal depression. In other cases merely a thin septum separates the anal depression from the termination of the rectum. In extreme cases, which are by no means rare, no anal depression is formed and the sacral part of the rectum is absent.

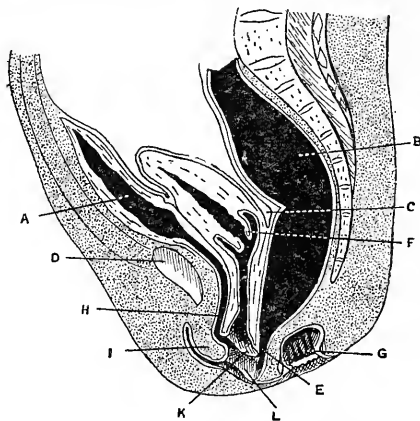


FIG. 409.—Section of Pelvis of Female Infant, showing the Rectum opening into the Navicular Fossa of the Vulva. *A*, bladder; *B*, rectum; *C*, recto-uterine fold; *D*, symphysis; *E*, vulval anus; *F*, cervix; *G*, anal depression (rarely present if rectum opens in vulva); *H*, urethra; *I*, clitoris; *K*, hymen; *L*, Labium minus.

There is some confusion as to how much of the anal canal is formed from rectum and how much from anal depression. As may be seen from Figs. 408 and 409 certain folds are formed in the wall of the anal depression. At the upper end of these anal folds, which are scarcely recognizable in

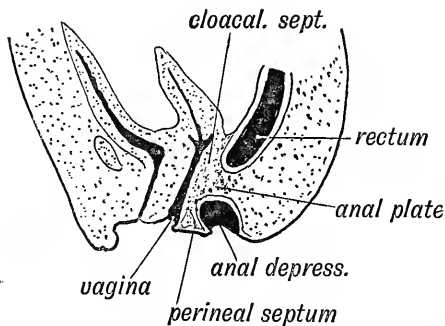


FIG. 410.—A Case of Imperforate Anus in which the Rectum has been arrested in its migration from the Cloaca to the Perineum.

the fully developed anal canal, are developed certain valve-like folds of mucous membrane, the **anal valves**. Above the valves are the well-marked columns of Morgagni formed in the rectum. The valves mark the junction of the rectum with the anal depression.¹

¹ See research by F. P. Johnson, *Amer. Journ. Anat.* 1914, vol. 16, p. 1.

External Genital Organs and Perineum.—That the interpretation just given of the embryological parts entering into the formation of the rectum and urethra is right is seen when the development of the external genital organs is traced. The stages in the development of the human urethra, penis and scrotum during the latter part of the 2nd month and earlier part of the 3rd are shown in Fig. 411. Stage I. represents the condition seen in the perineum about the end of the 8th week. The circular fold *A*—cloacal fold¹ it may be named, for it represents the opening or margin of the primitive (ectodermal) cloaca. Within its anterior

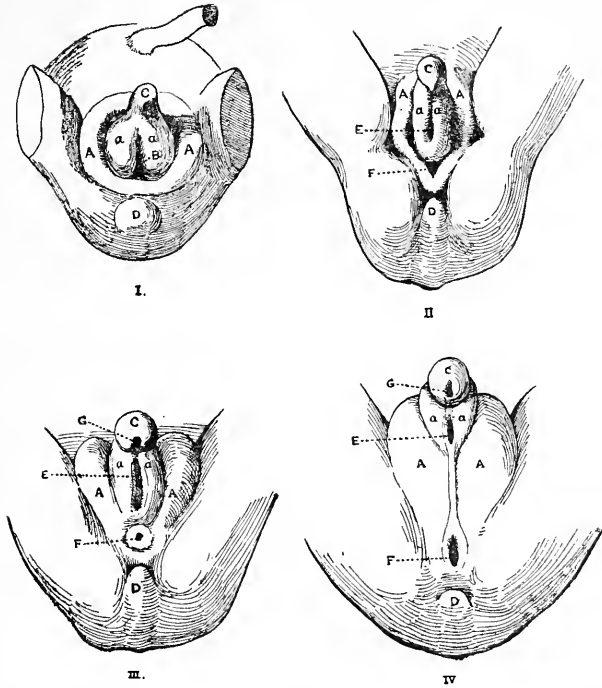


FIG. 411.—Stages in the development of the Human Penis and Perineum. (Drawings by Dr. Stanley Beale after figures given by Kollmann, Keibel and Hertzog.) I. human embryo 25 mm. long (8 weeks); II, 29 mm. long (9th week); III, 31 mm. long (9th week); IV, 45 mm. long (about 10th week). *A*, lips of cloaca (labia majora); *B*, urogenital orifice being carried to the surface between labia minora (*a, a*); *C*, penis becoming extra-cloacal; *D*, Tail; *E*, urogenital orifice; *F*, anus; *G*, meatus.

or pubic fornx is rising up the genital eminence to form the penis or clitoris—according to sex, for at this time the external parts of both sexes are alike, although the ovary is being differentiated from the testicle. There is a groove or furrow on the under or cloacal aspect of the genital eminence, as on the cloacal penis of the tortoise; it represents the roof of the penile urethra, and leads backwards to the urogenital sinus. The folds at each side of the furrow (*a, a*) are the vestibular or **perineal folds** which form the penile urethra in Echidna. In Stage II. (Fig. 411), reached

¹ Usually named the outer genital fold.

during the 9th week, two further changes are seen in progress. The lateral perineal folds (*a, a*) have now united behind the genital or urethral furrow, and by so doing have separated the anal part of the ectodermal cloaca (perineal depression), in which the rectum now terminates, from the anterior urogenital part. By the union of the posterior ends of those lateral perineal folds the perineal body is formed. The cloacal folds (*A, A*) are still well marked, but it is apparent that the genital eminence and its attached folds are being extruded from the cloaca. In Stage III., reached at the commencement of the 3rd month, a condition is represented which is common to both male and female foetuses. The anus is now extruded from its depression, and lies within the flattened posterior fornix of the cloacal folds. The lateral perineal or vestibular folds meet behind in the perineal body, where their free margin forms a semilunar fold—the primitive fourchette. Anteriorly the folds unite on the perineal aspect of the glans. Between the folds opens the penile urethra; the opening between the folds is the orifice of the urogenital sinus; it represents the primitive meatus of the penile urethra. On the under or perineal aspect of the glans a depression (the phallic groove) packed with an ectodermal plug is also present; it forms the part of the urethra within the glans. Stage IV. represents a condition peculiar to the male. A median raphe or suture is now seen extending from the anus behind to terminate in front in the two perineal or vestibular folds—perhaps it would be well to name their anterior parts, which are confined purely to the urethra of the male and vestibule of the female—urethral or inner genital folds. The primitive urethra is now small in size and well advanced towards the glans penis. The median perineal raphe is caused by a fusion of the tissues of the cloacal or outer genital folds within the septum primarily formed by the union of the lateral perineal folds. In the female this union of the cloacal folds does not occur, and hence there is no raphe on the female perineal body (Wood Jones). The cloacal folds remain separate, and form the labia majora; in the male they unite, and form the scrotum.

By the end of the 3rd month the process of union which gives rise to the perineal raphe extends to the glans, and in this way the primitive meatus is closed, the terminal parts of the vestibular folds forming the frenum of the prepuce. Thus the anterior parts of the perineal folds unite right up to the fraenum of the prepuce, and enclose the male urethra. In Stage IV. (Fig. 411) the margins of the phallic groove on the glans have united; the plug of epithelium within it breaks down as it unites with the cloacal urethra, and the permanent terminal urethra and meatus are thus established. In Stage IV. the preputial collar of skin is seen in process of formation. It is directly continuous with the anterior ends of the folds surrounding the primary meatus. It does not rise up as a free fold; ¹ the epithelium on the deep surface of the collar adheres to that on the glans, and hence when the prepuce is fully formed in the 4th month, the prepuce is tightly bound to it until the period of birth.

¹ Dr. Berry Hart (*Journ. Anat. and Physiol.* 1908, vol. 42, p. 50) and Dr. Wood Jones (*Brit. Med. Journ.* 1910, Jan. 15th) give another interpretation of the manner in which the prepuce is formed.

Hypospadias.—It is not unusual to see cases in which the process of urethral development has been arrested. In the female its complete arrest is normal; in individuals with imperfect differentiation of sexual glands (usually imperfect males) the process is also arrested at an early stage. Fig. 412 represents three conditions of hypospadias due to arrest

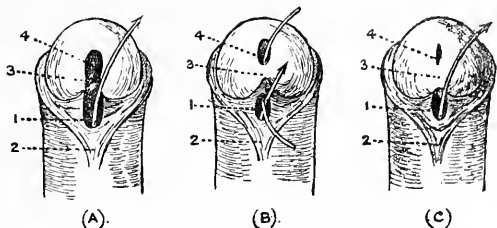


FIG. 412.—Three types of Hypospadias—*A*, in which the Groove in the Glans (phallic groove) is open, and Urine passes by the primitive meatus; *B*, in which the floor of the Phallic Groove is formed, but the primitive meatus is unclosed; *C*, in which the Phallic Groove is unformed or obliterated and the primitive meatus persists. 1, Primitive meatus; 2, fraenum praeputii; 3, phallic groove and canal; 4, permanent meatus.

of development at the terminal stage. In *A* the phallic groove is unclosed; the urethra opens at the primary meatus; the folds bounding the meatus represent the anterior ends of the urethral or perineal folds. In *B* the primitive meatus is unclosed, but the phallic groove is converted into a canal; in *C*, the commonest type, the primitive meatus is open and the phallic groove has remained uncanaliculized.¹

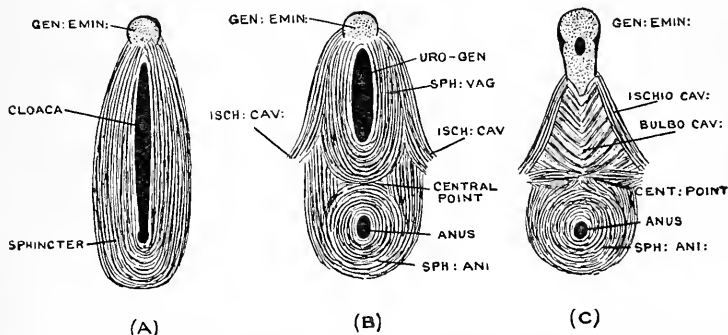


FIG. 413.—Stages in the Evolution of the Perineal Musculature. (After Popowsky.) *A*, sphincter of the cloaca in the 2nd month; *B*, its division at the beginning of the 3rd month; *C*, its condition in the male foetus at the end of the 3rd month.

Perineal Muscles.—From what has been said regarding the cloaca, the evolution of the muscles of the perineum from the sphincter of the cloaca will be readily understood. The sphincter in cloacal vertebrates surrounds the part of the cloaca (perineal depression) formed from ectoderm; it is a striated muscle. At the end of the 2nd month this muscle is apparent in the cloacal fold of the human foetus (Fig. 413, *A*). At the beginning of the 3rd month, when the perineal body is formed, the sphincter of the

¹ See Ralph Thompson, *Journ. Anat.* 1919, vol. 53, p. 32.

cloaca becomes divided into urogenital and anal parts¹ (Fig. 413, *B*). The sphincters of the urogenital passage and anus fuse in the perineal body. A part of the urogenital sphincter obtains an attachment to the ischium and forms the ischio-cavernosus (erector penis); another strand, the transversus perinei. With the formation of the urethra in the male, the sphincter of the urogenital passage is carried forwards on the bulb and forms the bulbo-cavernosus; in the female it remains as the sphincter vaginae. A deeper and older part surrounds the upper part of the urogenital sinus, and becomes the constrictor urethrae.

Origin of the Bladder.—In amphibians the bladder is a diverticulum of the cloaca. In the embryos of reptiles, birds and mammals it becomes modified, to form the allantois; part lies outside the body and is lost at birth, part remains within the body to form the urachus and all the bladder except the trigone. By a downward migration of the orifices of the Wolffian and Müllerian ducts, the upper part of the urogenital sinus, containing the insertion of the ureters, remains to form the trigone of the bladder and supra-genital part of the urethra (Figs. 388, 407).

The Urachus.—When the body stalk becomes elongated in the formation of the umbilical cord, the part of the allantoic cavity within it is obliterated. The part of the allantois within the abdomen, stretching from the umbilicus to the apex of the bladder, becomes the urachus, a fibrous cord, in which all trace of the allantoic cavity is lost (Fig. 416). Occasionally traces of the cavity may remain and form **urachal cysts**,² or it may remain open throughout, so that urine escapes from the bladder by a fistula at the umbilicus. The urachus lies behind the linea alba, embedded in the subperitoneal tissue, and flanked on each side by the umbilical artery. In the 7th month the apical part of the bladder is attached by a mesentery to the anterior wall of the abdomen; later the mesentery disappears (Broman).

The Bladder at Birth.—At birth the bladder is elongated and fusiform in shape, with a small trigone (Fig. 416). The capacity of the pelvis is relatively less than in the adult; hence the greater part of the bladder is supra-pubic in position.

Ectopia vesicae³ is not easily explained on an embryological basis. The condition is shown diagrammatically in Fig. 414, *A*. The anterior wall of the bladder and roof of the urethra and the parts of the belly wall in front of these are absent; the trigone, floor of the urethra, and posterior wall of the bladder are flush and continuous with the belly wall. The symphysis pubis is not formed. Certain chambers in the embryo, such as the neural canal and pericardium, are liable to a dropsy and rupture. Were the cloaca of the embryo to become ruptured along its ventral wall (Fig. 414, *B*) the condition of ectopia would be produced. Further, it is

¹ W. J. Otis, *Anat. Hefte*, 1905, vol. 30, p. 199 (Dev. of Anus and External Sphincter).

² See Alban Doran, *Proc. Roy. Soc. Med.* April, 1908.

³ For current theories see Wood Jones, *Journ. Anat. and Physiol.* 1912, vol. 46, p. 193; Keith, *Brit. Med. Journ.* 1908, Dec. 26th; A. M. Paterson and Emrys-Roberts, *Journ. Anat. and Physiol.* 1906, vol. 40, p. 332.

to be remembered, as Berry Hart has pointed out, that the part of the embryo on which the primitive streak is situated comes to form the post-umbilical part of the ventral wall of the abdomen (see page 37). It is therefore more probable that the condition may be due to an unclosed condition of the primitive streak.

Musculature of the Bladder, Urethra and Rectum.—Seeing that the rectum, allantois and cloaca are continuous in the embryo one would expect that the musculature of the parts should show traces of this continuity. Mr. F. Wood Jones found (1) that the band of musculature which passes from the front of the rectum to be lost in the tissue behind the membranous urethra is a remnant of the recto-cloacal communication in the embryo (Fig. 408); (2) that the circular muscular coat of the urethra is continuous above with the sphincter and circular coat of the bladder,

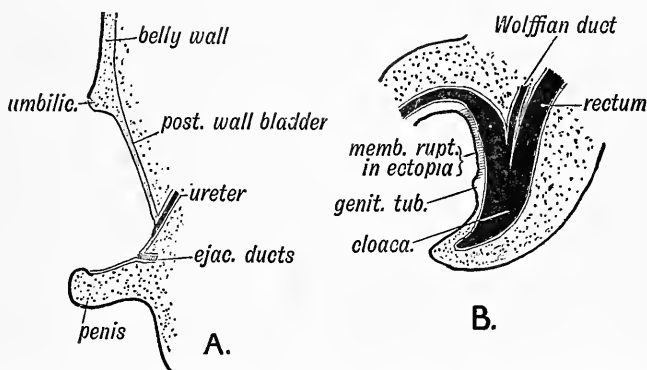


FIG. 414, A.—A Section to show the condition of parts of Ectopia Vesicae.

B.—Section of the Pelvis of an Embryo (5th week) to show how the condition is probably produced.

and below it becomes continuous with the striated fibres (constrictor urethrae) surrounding the membranous urethra. The latter, however, are not developed from the musculature of the urogenital sinus, but from the sphincter cloacae (Fig. 413).

Neurenteric Canal.—Ano-coccygeal tumours are believed to arise from remnants of the neurenteric canal as well as from the post-anal gut. The neurenteric canal, or blastopore, it will be remembered (p. 38), is a communication of the cavity of the archenteron with the dorsal surface of the embryo. The blastopore opens at the anterior end of the primitive streak, which afterwards is included in the posterior end of the neural groove; such a canal might be represented by a remnant passing from the rectum to the sacral region of the spinal canal. A vestigial structure, which is certainly of this nature, has not so far been recognized. The part of the hind-gut which is developed under the tail of the embryo (post-anal gut) disappears in the 2nd month of development, but certain congenital tumours which arise between the sacrum and coccyx may spring from remnants of the **post-anal gut** (p. 381). Seeing that the embryonic tissue which gives rise to the caudal end of the body lies in the posterior lip of

the blastopore, it is not difficult to conceive that embryological remnants might persist in the sacro-coccygeal region of the pelvis and give rise to teratomatous tumours.

External Genitals of the Female.—In the female the parts retain closely the early foetal form represented in Fig. 415. The genital tubercle becomes the glans clitoris. In the genital eminence—of which the tubercle is merely the summit—the corpora cavernosa develop. The vestibular or inner genital folds form the **labia minora**, the prepuce and fraenum. By the junction of the inner genital folds within the urogenital depression behind, the **fourchette** is formed. Thus the opening into the urogenital sinus (primitive meatus) is bounded by the fourchette, labia minora and fraenum of the prepuce. In the lateral folds, or labia minora, are developed the bulbs of the vestibule. After the third month the external genital (cloacal) folds become prominent around the urogenital depression and form the labia majora. By their anterior union they give rise to the mons

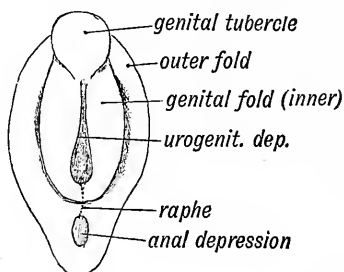


FIG. 415.—Diagram showing the terms usually applied to the External Genital Parts of the Embryo. The outer genital represent the cloacal folds; the inner genital folds the anterior parts of the vestibular folds; the urogenital depression or cleft, the primary meatus (see Fig. 411).

veneris. Their posterior extremities fade away posteriorly (Fig. 411). After the 3rd month the external genital parts undergo a change directly opposite to that which takes place in the male. The primary meatus and penile urethra open up and form the vestibule, into which open urethra and vagina. This change is probably due to the influence of the ovarian germinal tissue.

External Genitals of the Male.—In the male, at the end of the 2nd month, the inner genital folds corresponding to the fourchette and labia minora, grow forwards as a crescentic shelf, thus closing the urogenital cleft and forming the floor of the penile urethra. While the floor of the penile urethra is formed thus, its roof, corresponding to the vestibule of the female, is derived from the urethral or forward prolongation of the cloaca (see Fig. 407). The erectile tissue in the inner genital folds, which forms the bulbs of the vestibule in the female, forms the corpus spongiosum in the male. The corpora cavernosa are formed in the genital eminence. The anterior part of the corpus spongiosum is formed separately in the apical part (glans) of the genital eminence. The corpora cavernosa are developed by the enlargement of capillary vessels of the body of the genital eminence during the 4th month. The part of the urethra within the glans

is the last part to be formed, and its development, as we have seen, is peculiar (p. 389). The part of the urethra within the glans becomes canalicularized a short time before birth. The fossa navicularis and lacuna magna occur at the junction of the part of the urethra formed in the glans and the part formed from the urogenital sinus.¹

The **scrotum** is formed during the 3rd month by the union of the external genital folds (labia majora of the female), the raphe formed by their union

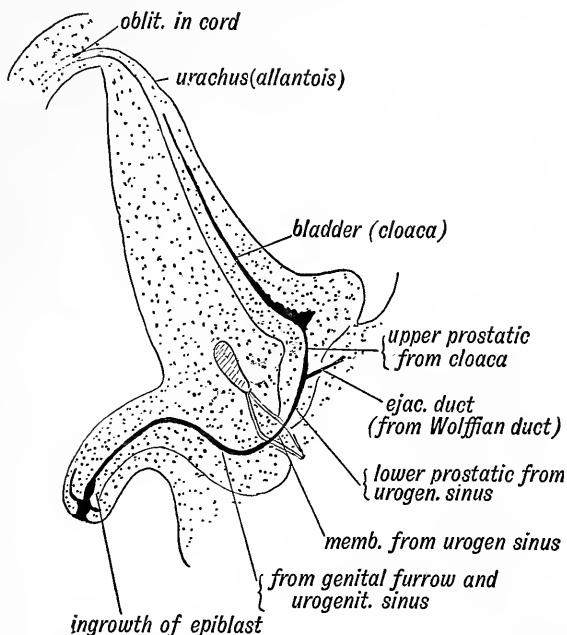


FIG. 416.—A Section of the Male Bladder and Urethra at Birth, showing the derivation of parts.

extending from the fraenum of the prepuce in front to the anterior margin of the anus behind (see p. 388).

THE PROSTATE.

The **prostate**² is developed by outgrowths of the entodermal lining the upper part of the urogenital sinus and from the mesodermal tissue surrounding the sinus. It consists of glandular tissue and stroma.

(1) The **glandular tissue** is composed of tubular glands which open into the prostatic part of the urethra. They are developed in the 4th month, as a series of solid buds, about 60 in number, from the epithelium lining

¹ For literature on development of urethra see A. Lichtenberg, *Anat. Hefte*, 1906, vol. 31, p. 63; J. E. Spicer, *Journ. Anat. and Physiol.* 1909, vol. 43, p. 195.

² For papers on the development of the prostate see E. J. Evatt, *Journ. Anat. and Physiol.* 1909, vol. 43, p. 314; 1911, vol. 45, p. 122.

the upper part of the urogenital sinus (Fig. 417). The buds, which soon become tubular in form, arise from a right and left longitudinal furrow or fold of the wall of the sinus between which the Wolffian ducts open (Pallin).

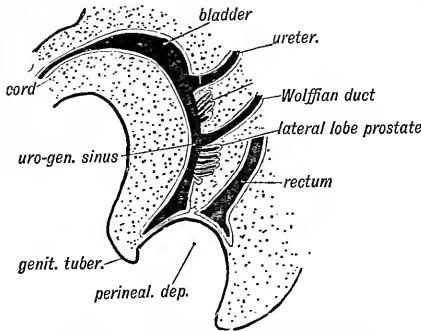


FIG. 417.—A Diagram to show the position at which the Prostatic Tubules arise.

The prostatic furrows reach upwards above the Wolffian openings into the purely urinary part of the sinus and downwards into the part which serves as a common passage for the semen and urine. These segments of the sinus become the **upper and lower parts** of the prostatic urethra. The buds from the right and left furrows form two lateral masses or lobes. At first the two lateral lobes, as in mammals generally, lie separately behind the urethra. Other outgrowths also arise from the anterior or pubic side of the sinus—some of these afterwards undergo atrophy—from the side or lateral aspect of the sinus (Fig. 418). The lateral prostatic masses fuse behind the urethra; in man only do they meet to form an anterior or pubic commissure over

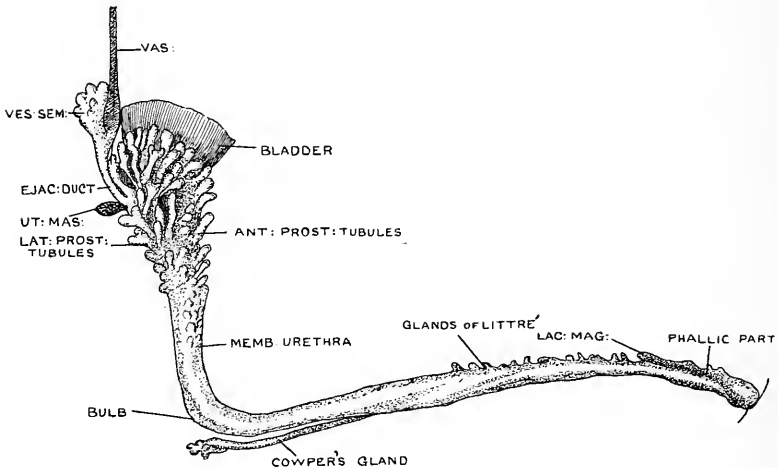


FIG. 418.—The Prostate and Urethra towards the end of the 4th month. (After Broman and Evatt.) The phallic part of the urethra ends posteriorly at the lacuna magna. It is developed in the glans. The uterus masculinus (ut. mas.) is indicated diagrammatically to show its relationship to the common ejaculatory duct.

it. The tubules of the median or third part arise from the middle line of the floor of the sinus above the openings of the Wolffian ducts (ejaculatory ducts) (Evatt), but the lateral lobes also fuse with this median element, and help to form it. It may be small or even absent.¹

¹ J. W. Thomson Walker, *Journ. Anat. and Physiol.* 1906, vol. 40, p. 189; O. S. Lowsley, *Amer. Journ. Anat.* 1912, vol. 13, p. 299.

Skene's tubules, which may be found opening into the urethra of the female, represent prostatic tubules. A reference to Figs. 408, 409 will show that the female urethra corresponds to the upper prostatic urethra of the male, and that the floor of the vestibule—in which rudiments of prostatic tubules may be formed—represents the lower prostatic urethra.

(2) **The Stroma of the Prostate.**—While the glandular tubes arise in linear groups from the epithelium lining the urogenital sinus—the muscular and fibrous elements arise from the mesodermal tissue of the genital cord in which the terminal parts of the Wolffian and Müllerian ducts are situated and from the circular musculature of the urogenital sinus (see Fig. 419). When the glandular elements grow out they become embedded in and carry

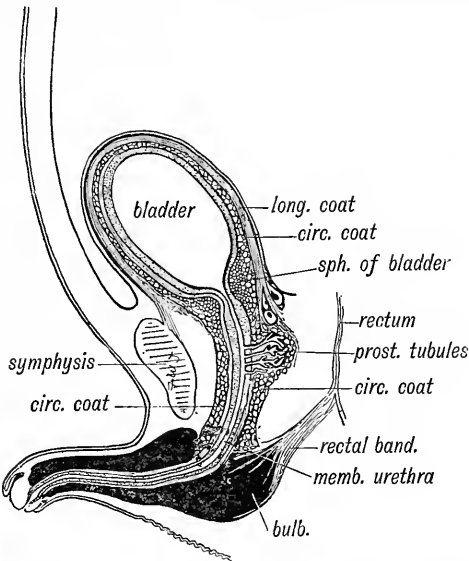


FIG. 419.—Diagrammatic Section of the Bladder and Urethra of a 6th month Foetus to show (1) the development of the Prostate, (2) the relationship of the Prostatic Musculature to that of the Urethra and Bladder. (Wood Jones.)

before them the circular musculature of the urogenital sinus which thus forms the muscular cortex or inner capsule of the prostate. Probably the stroma of the genital cord also contributes to the musculature of the prostate. The musculature of the uterus, which is also developed from the genital cord, like that of the prostate, is liable to become the seat of fibromyomatous growths in the later years of adult life.

As regards the nature of the prostate :

(1) It is purely genital, and develops only in the rutting season in such mammals as manifest a seasonal sexual life. Its development in the female is arrested at a very early stage—probably the result of an ovarian influence.

(2) It remains comparatively undeveloped until puberty. At the age of seven it weighs only 30 grains ; after sexual life is established it weighs about 300 grains.

(3) The healthy prostate atrophies if castration is performed, but this operation has no effect on glands which have become pathologically hypertrophied.¹ In one man out of three over 55 years of age the prostate hypertrophies, both the glandular and fibro-muscular elements participating. Hypertrophy of the median part causes a valvular elevation behind the vesical opening of the urethra.

Glands of Cowper and Bartholin are produced as solid buds from the entodermal lining of the penile extension of the urogenital sinus (Fig. 418). Hence in the female the ducts of Bartholin's glands open in the vulval cleft just outside the hymen at each side of the vagina, for the hymen marks the junction of the Müllerian ducts with the urogenital sinus. In the male the ducts of Cowper's glands open in the bulbous part of the urethra (Fig. 418). Their function is unknown, but they are certainly sexual in nature. The numerous **glands of Littré**, like Cowper's and Bartholin's glands, are produced by tubular outgrowths during the fourth month (Fig. 418). In the male the glands of Littré are produced most numerous along the dorsal aspect of the urethra.

Round the anus, and especially in the furrow between the labium minus and majus, groups of large peculiar sebaceous glands are produced in the 4th and 5th months, corresponding to the **anal** and **preputial** glands of mammals. Occasionally two groups of sebaceous glands occur on the prepuce of the male, especially if hypospadias be present (Shillitoe). Glands round the corona of the glans penis (**Tyson's glands**) are only very exceptionally present.

THE TESTES.

Descent and Development of the Testicle.²—The origin of the testis on the inner or mesial side of the Wolffian ridge, and its attachment to the dorsal wall of the coelom by a mesentery common to it and the Wolffian body have been already described (see Figs. 4, 23, 384). The position of the testicle in a foetus of the third month is shown in Fig. 420. Although in the 6th week the genital ridge extended from the 6th to the 12th thoracic segment, the testicle, developed from the hinder part of the ridge, is now situated in the iliac fossa. The mesorchium, a fold of peritoneum, binds its attached border to the iliac fossa. At its outer side lies the genital part of the Wolffian body which forms the epididymis. It, also, is suspended by a mesentery—the Wolffian mesentery. The two mesenteries have a common base—the common urogenital mesentery (see Fig. 384). The upper part of the urogenital mesentery forms the diaphragmatic fold, with which the peritoneal fold containing the spermatic artery becomes joined; to the combined fold is given the name of **plica vascularis** (compare

¹ E. Pittard, *Compt. Rend. Acad. Sc.* 1911, vol. 152, p. 1617 (Effect of Castration); Cuthbert S. Wallace, *Trans. Path. Soc. Lond.* 1905, vol. 56, p. 80; W. L. H. Duckworth, *Journ. Anat. and Physiol.* 1906, vol. 41, p. 30 (Eunuchoid Man); R. H. Whitehead, *Anat. Rec.* 1908, vol. 2, p. 177, *Amer. Journ. Anat.* 1905, vol. 4, p. 193 (Dev. and Nature of Interstitial Cells).

² See Eben C. Hill, *Amer. Journ. Anat.* 1907, vol. 6, p. 439 (Dev. of Blood Supply); D. T. Barry, *Journ. Anat. and Physiol.* 1910, vol. 44, p. 137 (Differentiation of Tubules).

Figs. 421, 424). This in the female becomes the ovario-pelvic ligament (Fig. 5). A fold of peritoneum, the inguinal fold or *plica gubernatrix*, continues the common urogenital mesentery to the groin (Fig. 420). The gubernaculum testis is developed in the *plica gubernatrix*; in the corresponding fold in the female the round ligament of the uterus appears (see p. 371). The vas deferens (Wolffian duct) turns into the pelvis from the lower end of the epididymis (Wolffian body), and within the pelvis lies in the genital cord (Fig. 392). A remnant of the Müllerian duct lies along the inner and ventral aspect of the epididymis.

Seminiferous Tubules.—The arteries for the genital glands represent the lowest of the vessels which originally supply the Wolffian body and arise from the aorta at the level of the 12th dorsal vertebra; their nerve supply comes from the 10th dorsal segment of the spinal cord. The testis is therefore developed in the genital ridge between the 10th and 12th

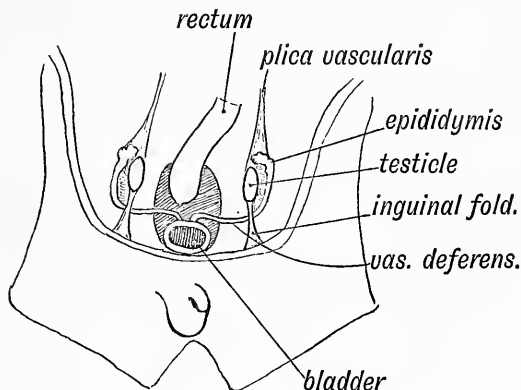


FIG. 420.—The Position of the Testis in a Foetus of 2½ months.

dorsal segments. The early development of the testis is similar to that of the ovary. Up to the 7th week, when the embryo measures 15 mm. in length, it is impossible to tell testicle from ovary; both of them at this time show a covering of germinal epithelium and deep central masses or columns of epithelioid cells derived from the covering layer of germinal epithelium. In the central masses are the large primitive germinal cells (primordial ova). At the end of the 7th week two changes lead to the differentiation of a testis from an ovary; (1) a tunica albuginea begins to form under the superficial epithelium, (2) the central masses proliferate and form radiating cords which branch and anastomose as they spread from hilum to periphery. The cords become transformed into the seminiferous tubules which are at first solid. Some of the epithelioid cells are not included in the tubes and remain to form **interstitial cells**.¹ The genitaloid cells are included in the epithelial cords. The tubules become separated into groups or compartments in the 6th month and about the

¹ See articles by Sir F. W. Mott, *Brit. Med. Journ.* 1919, vol. 2, p. 655; T. Russell Goddard, *Journ. Anat.* 1920, vol. 54, p. 173; B. F. Kingsbury, *Amer. Journ. Anat.* 1914, vol. 16, p. 59.

same time lumina are formed in them. The formation of spermatozoa has been already described (p. 9). The visceral layer of the tunica vaginalis on the testicle represents the covering of flattened epithelium which remains after the ingrowth of the germinal epithelium. The vasa efferentia and coni vasculosi are formed from the **genital** Wolffian tubules ; the rete testes and vasa recti from the junctional cords (p. 361). Into the rete open the tubuli seminiferi formed in the testicle. The epididymis is the elongated upper segment of the Wolffian duct (Fig. 386). The Wolffian elements are produced within the Wolffian ridge (Fig. 390).

Formation of the Gubernaculum Testis.¹—There is no trace of the inguinal canal in the 3rd month of foetal life ; the various layers of abdominal wall are unbroken, except for a fine strand of tissue which leads

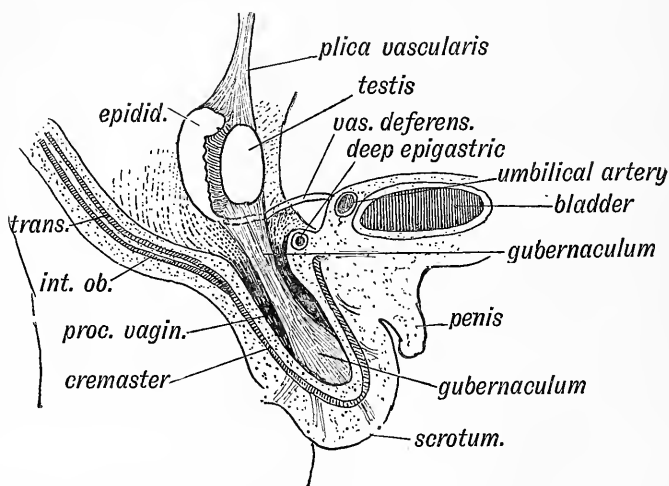


FIG. 421.—Showing the Position of the Testis at the 6th month, and the Formation of the Gubernaculum Testis.

towards the site of the scrotum, and evidently serves as a guide for the gubernacular outgrowth. In the fourth month the subperitoneal layer of non-striated muscular tissue in the plica gubernatrix and in the mesorchium takes on a rapid growth (Fig. 421). At the same time the tissues of the abdominal wall undergo a localized evagination towards the scrotum. They are probably carried down by the growth of the gubernacular bud which pushes its way to the scrotum. The gubernaculum grows downwards as a solid cellular mass, until it reaches the subcutaneous tissue which at that time completely fills the scrotum. Its attachment to the scrotum is slight and easily broken (Fig. 421). The gubernaculum, as it grows through the abdominal wall, carries with it :

(1) A process of peritoneum (the processus vaginalis) ; (2) The transversalis fascia (the infundibuliform fascia) ; (3) The internal oblique and transversalis muscles to form the cremaster ; (4) The spermatic fascia

¹ See John Hunter's classical account, Palmer's Edition of his Works, vol. 4, 1837. Also paper by Dr. Berry Hart, *Trans. Edin. Obstet. Soc.* 1909, vol. 34, p. 151.

from the external oblique; (5) The deep layer (Scarpa's) of the superficial fascia of the groin. All these layers are added to the primitive coverings of the scrotum, which until then is made up simply of skin and superficial fascia (Fig. 421).

It will thus be seen that the gubernaculum testis is a fibro-muscular mass with an actively growing cellular cap, which, starting from the muscular stratum in the mesorchium and plica gubernatrix in the iliac fossa, invades the abdominal wall, every layer of which it carries as a prolongation within the scrotum. It is an invading army of cells. It draws with it into the scrotum the peritoneum in the iliac fossa, on which the testis is dragged like a log on a sledge.

The testis descends from the loins to the iliac fossa in the 3rd month; from the 4th to the 7th month it rests at the site of the internal ring;

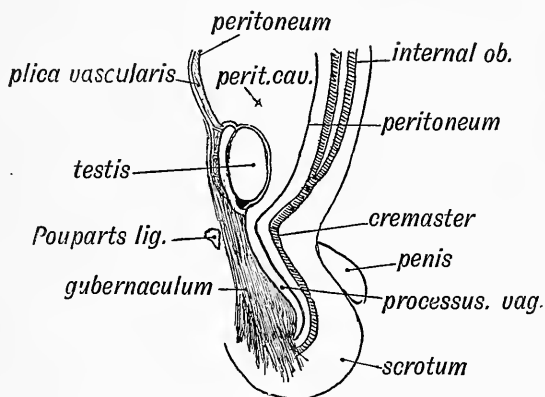


FIG. 422.—The manner in which the Structures in the Wall of the Abdomen are carried out so as to form the Inguinal Canal and Coverings of the Testis.

it spends the 7th month of foetal life in its exodus through the abdominal wall. In the 8th month it leaves the inguinal canal and lies at the external abdominal ring. After birth it reaches the fundus of the scrotum. The atrophy and contraction of the gubernaculum pull it down. A remnant of the gubernaculum can always be found in the adult behind the epididymis and testicle, within the mesorchium (Fig. 423).

Processus Vaginalis.—The processus vaginalis becomes occluded by adhesion or zygosia (p. 287) at two points soon after birth, but in a considerable proportion of individuals the process of closure is delayed (Fig. 423). The upper point of occlusion takes place at the internal abdominal ring; the lower a short distance above the testicle. The part of the processus vaginalis between the points of occlusion is known as the **funicular process**; the part surrounding the testicle becomes the **tunica vaginalis**. In quite 30% of children the occlusion takes place at the internal abdominal ring some considerable time after birth or it fails to appear altogether. Occlusion may fail at the upper point, at the lower point, or at both. Or it may close at both points, but the funicular process, instead of disappearing, may remain open and form a cyst.

Descent of the testicle¹ may be arrested at any stage; often in the inguinal canal; more frequently at the external abdominal ring. Arrest of descent is commonly regarded as a symptom of arrest of testicular development. John Hunter regarded arrested descent of the testicle as due to an imperfection in its development; all recent observations support his opinion. There can be no doubt that in all those mammals² in which the testis leaves the abdomen it does so to escape the intra-abdominal pressure to which the abdominal viscera are subjected. Its descent is correlated with the evolution of the diaphragm and exclusion of the lungs from the abdominal cavity. Violent respiration and flexure of the trunk give rise to very high degrees of tension within the abdomen; from some cause at present not understood, a testicle atrophies when subjected to

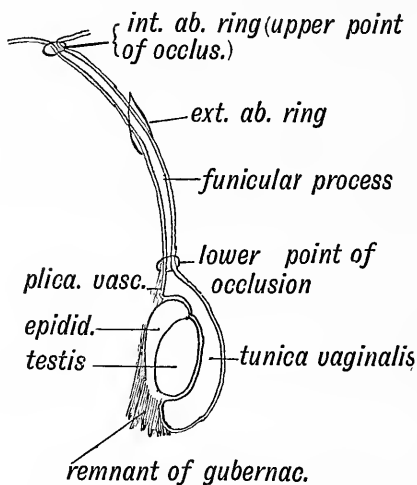


FIG. 423.—A Diagram of the Processus Vaginalis.

this pressure. On the other hand, the testicle may assume an **ectopic** position. The gubernaculum, as it makes its way towards the scrotum, may take an eccentric course, and bring the testicle to rest in the groin, root of the penis, or over the pubis.

Mesorchium.—The testis and epididymis were suspended within the abdomen by the common urogenital mesentery (Fig. 384). In the course of the descent of the testis this becomes shortened by the development of the gubernaculum, and the testis and epididymis become thus firmly bound by their posterior borders to the tunica vaginalis. The digital fossa, situated between the mesorchium and mesentery of the Wolffian body, represents the recess which separated the genital from the Wolffian ridge of the embryo. The mesorchium—the true mesentery of the testicle—may assume the form of an elongated fold, attaching the testicle to the epididymis (Corner).

¹ D. Berry Hart, *Journ. Anat. and Physiol.* 1910, vol. 44, p. 4.

² See W. N. F. Woodland, *Proc. Zool. Soc. London*, 1903, vol. 1, p. 319.

A not unusual anomaly of the testicle is represented in Fig. 425. It will be observed that the common mesentery, in place of becoming shortened, and thus fixing the testicle and epididymis widely to the peritoneum, becomes narrow and elongated. Such testicles are usually arrested in their descent, and are apt to twist and become strangulated. It will also be observed that a gubernaculum is present, but it has seized and drawn downwards only a loop of the vas deferens. The explanation is shown in Fig. 424. The inguinal fold is made up of two parts, **a lower**, ending on the vas deferens and corresponding to the round ligament of the female; **an upper**, which continues the fold to the epididymis and testicle, and

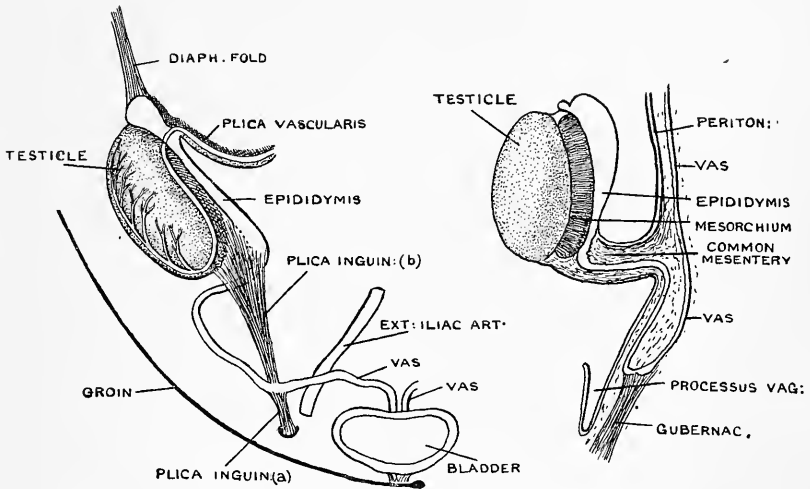


FIG. 424.—To show the Diaphragmatic Fold (upper part of the common genital mesentery), Vascular Fold, and the two parts of the Inguinal Fold in a Foetal Fig. (Eben. C. Hill.)

FIG. 425.—Elongated Common Mesentery of a Testicle arrested in the course of its descent.

which corresponds to the round ligament of the ovary. In such cases, then, the gubernaculum has not extended to the upper part of the inguinal fold.

Hermaphrodites.¹—A hermaphrodite—a human individual in which both testis and ovary are present—has never been seen. Dr. Bulloch found only five cases on record in which, within the same genital gland, there were present representations of imperfect testicular and ovarian tissues (ovario-testis); spermatozoa and ova were not present. The term is usually applied to individuals in whom the genital glands are imperfectly developed. Usually they are imperfect males. It is clear that sexual differentiation commences in the 7th week (although the sex is probably determined at, or even before the time of fertilization); by some

¹ See Bulloch, *Treasury of Human Inheritance*, London, 1909, Part 3, Section Xa; Berry Hart, *Proc. Roy. Soc. Edin.* 1909, vol. 29, p. 607, 1910, vol. 30, p. 230; J. F. Gudernatsch, *Amer. Journ. Anat.* 1911, vol. 11, p. 267; F. R. Lillie, *Journ. Experim. Zool.* 1917, vol. 23, p. 371.

means—probably by an internal secretion—the ovarian and testicular tissues exercise a direct and opposite influence on the development of genital structures. Hence, if the gland is imperfect, development of the genital parts is uncontrolled and represents a condition which may best be described as neutral. There is evidence to support the opinion that the embryonic genital gland is composite; the testicle develops within the medullary or central part of the gland; the ovary from its cortical or more superficial parts.

Development of the Suprarenal Bodies.—The suprarenal or adrenal bodies arise by the association of two distinct embryological elements—*cortical* and *medullary*. In Fig. 427 is given a diagrammatic section to show the stage reached in the 7th week of development, the cortical element then being large and projecting at the root of the mesentery and in contact with the genital and Wolffian bodies, while the medullary

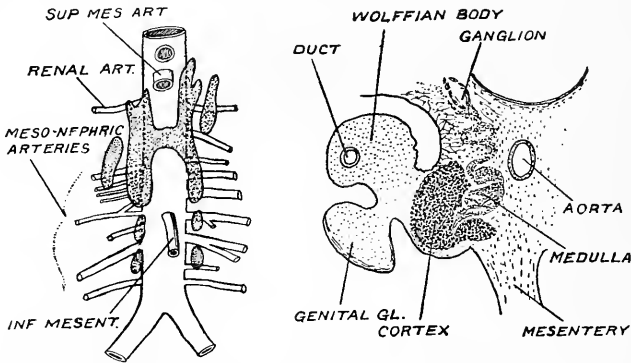


FIG. 426.—Showing the distribution of the aortic chromaffin bodies in the early human foetus. (After Zuckerkandl.)

FIG. 427.—Section across the suprarenal, genital and Wolffian bodies in an embryo in the 7th week, 15 mm. long. (After Zuckerkandl.)

element consists of indifferent cells connected with the blastema of the sympathetic system. The **cortical element** is associated with the genital system; its secretion regulates the development of certain sexual structures and functions. Like the epithelioid cells of the genital glands, the cortex arises by an invagination of coelomic epithelium, the suprarenal ingrowth occurring on each side of the root of the mesentery early in the 6th week. The suprarenals are developed within the anterior ends of the Wolffian bodies, just behind the pleuro-peritoneal passages. The **medulla** arises from groups of cells which also form sympathetic ganglia; probably from the primitive cell basis of the semilunar ganglion, which is developed by the side of the aorta, close to the pleuro-peritoneal opening. Hence the great plexus of nerves which passes from the solar plexus to the medulla of the suprarenals. The medullary cells begin to migrate into the cortex in the 8th week; the process of invasion is continued through the greater part of foetal life. The invading cells, when stationed in the cortex, give rise to broods of chromogenic cells and later to sympathetic nerve cells.

By the beginning of the 4th month they are arranged as reticulating columns set on the walls of branching venous sinuses.

The cortical cells range themselves in rows between radiating blood sinuses. As the kidneys ascend in the 3rd month they come in contact with the suprarenal bodies. The suprarenal is at first larger than the kidney, even at birth they are nearly equal in size. The nerves and arteries enter the bodies on their renal surface; the veins emerge on their anterior surface.

Until the 3rd month the suprarenal bodies are in contact with the upper pole of the testis or ovary. As the genital glands descend, the diaphragmatic fold is drawn from the suprarenal region and frequently carries with it buds of suprarenal tissue both cortical and medullary. It is therefore readily understood how isolated parts of the suprarenal body (accessory suprarenals) may occur in the broad ligament or in the spermatic cord above the testicle. Such accessory bodies are probably derived from the cortical element which is developed within the Wolffian ridge and body. With the descent of the ovary and testicle, which bring with them the Wolffian body, adjacent accessory suprarenals, if such be present, are also brought down, and may occasionally give rise to peculiar tumours.

Chromaffin Cells.¹—The medullary part of the suprarenals belongs to a segmental series of organs. In such fishes as the shark and lamprey, a group of cells (a paraganglion) is thrown off from each ganglion of the sympathetic chain and comes into close contact with the tributaries of the cardinal veins. These cells stain brown with salts of chromium—hence their name; some of these cells remain within the sympathetic ganglia. Similar minute chromaffin bodies (paraganglia) are also developed in or near all the ganglia of the vertebral chain of the human foetus. The carotid body arises in association with the upper cervical ganglion. Other collections of chromaffin cells arise at the sites of the prevertebral ganglia and plexuses—such as the superior and inferior mesenteric plexuses. The distribution of the aortic chromaffin bodies is shown in Fig. 426. Although chromaffin cells arise from the blastema of the sympathetic system yet they are differentiated before the nerve cells of that system, as if they represented the products of an earlier evolution. By their secretion they assist, or serve as substitutes for, the vasomotor sympathetic cells and for all nerve cells which have to do with regulating the action of non-striated muscle. The medulla of the suprarenal represents the brain of the chromaffin system, but why it should be associated with a cortical element has not yet received an explanation.

Coccygeal Body² is a small mass of chromaffin tissue, with rich blood supply, situated on the ventral aspect of the coccyx.

¹ For an account of chromaffin tissue see an article by Swale Vincent, *Journ. Anat. and Physiol.* 1904, vol. 38, p. 34; E. Zuckerkandl, *Keibel and Mall's Manual of Human Embryology*, vol. 2, 1912.

² J. Thomson Walker, *Archiv. für Mik. Anat. und Entwickl.* 1904, vol. 64, p. 121 (Coccygeal Body).

CHAPTER XXV.

BODY WALL AND PELVIC FLOOR.

Stages in the Evolution of the Body Wall.¹—Behind the apparently simple arrangement of structures in the body wall of man lies a long history, only some of the later stages being known to us. Even in the lowest vertebrates the wall surrounding the pericardial and abdominal cavities is already muscular. We presume, however, there was a stage in which they were devoid of muscle, for in all vertebrates the musculature which enters the somatopleure, the lamina which forms the body wall of the embryo, arises from the muscle plates of the somites placed along each side of the dorsal median axis of the embryo (see p. 68). In fishes the musculature of each side of the body wall is arranged in two systems: (1) a vertebral, lateral or oblique system in which the ribs are embedded; (2) a ventral or longitudinal system which extends from pharynx to tail. Both longitudinal and oblique systems are differentiated from one stratum. It is from a simple system of this nature that the musculature of the human body wall has been evolved (see Fig. 445).

Respiratory Stage.—With the evolution of lungs the musculature of the body wall assumed a respiratory function.² In fishes its chief use—if one excepts the part it plays in body movements—is to assist in the circulation of the blood within the body cavity—to drive it on towards the heart, and to expand or contract the cavity as the alimentary canal fills or empties. By means of ribs embedded in the septa of the lateral wall, the musculature of the body cavity became capable not only of compressing or diminishing the body cavity, but also of expanding it, and thus filling the lungs with air. In this manner the body musculature entered into the service of the lungs, and the nerve centres (respiratory centres) in the hind-brain, which formerly regulated the movements of the gills and pharynx, came to have an automatic dominion over musculature of the body wall. The ribs, which served in the simple economy of the fish's body, became strengthened and firmly jointed to the vertebrae; at the ventral ends of those encircling the lungs a supporting bar—the sternum—was evolved; the primitive sheets of musculature became differentiated to act on the ribs. In the latter part of the 2nd month

¹ See R. H. Paramore's "Hunterian Lectures," *Lancet*, 1910, May 21st and 28th; Prof. Wood Jones, *Journ. Anat.* 1913, vol. 47, p. 282.

² F. Tourneux, *Compt. Rend. Assoc. Anat.* 1902 (Dev. of Walls of Thorax).

when the lungs and pleural cavities are undergoing rapid development, respiratory transformations, similar in nature to those just mentioned, are taking place in the human embryo.

Mammalian Stage.—We have already seen that the lungs of mammals develop within special cavities, which ultimately surround the heart; as the pleural cavities expand they dislocate from the neck and depress within the body cavity a partition which completely divides it into thorax and abdomen. With the evolution of the diaphragm, and the disappearance of the lungs from the abdominal cavity, the body wall musculature became further modified, so that it can control the thoracic as well as the abdominal pressure. The evolution of pleural cavities effected a transformation in the thoracic part of the body wall. Their expansion and the differentiation of the thoracic wall are taking place during the latter part of the 2nd month of human development.

Orthograde Stage.—It is believed by many that the upright or orthograde posture is confined to man, and that it represents one of the more recently acquired human characters. This is certainly not the case; man shares the orthograde posture with the group of primates with which he has so many structural affinities—namely, the anthropoid apes. Like man, they carry their bodies in an upright posture during progression. The smallest and most primitive of the anthropoid apes—the gibbon—is of ancient origin; the orthograde posture is therefore an adaptation which has been long established in the higher group of primates. With a change of posture to the orthograde the action and fixation of the musculature of the body wall became greatly altered; the mechanism of respiration was necessarily altered. The chest became wide or barrel-shaped, the sternum broad; the heart came to rest on the diaphragm. The muscles of the abdominal wall had not only to carry on their respiratory function; they had also to support the abdominal viscera and to assist in emptying them. The mesenteric adhesions which take place during the early months of foetal life (see p. 286) are designed to give additional fixation to the viscera. The lower abdominal viscera came to rest on the pelvic floor; the muscles of the tail, which rise within the pelvis of pronograde mammals, were modified to form a muscular hammock for the support of the viscera and the external tail disappeared. The caudal or coccygeal vertebrae are more reduced in the anthropoid apes than even in man. The spinal musculature and spinal column were altered to meet the new postural conditions.

Plantigrade Stage.—If man shares the orthograde posture with a group of higher primates, the power of plantigrade progression is peculiarly his own. Everyone recognizes that the foot, the leg, the thigh of man have undergone extensive structural alterations, but the fact is often overlooked that the process of adaptation has also led to marked structural changes in the body wall. The inguinal region especially has been modified. The great development and complete extension of the thigh have altered the musculature of the groin; the inguinal (Poupart's) ligament has been evolved. These structural adaptations have weakened the human groin,

and made it the commonest site of hernia. In the normal human upright posture the trunk is balanced on the pelvis; the crest of the ilium and the external oblique have become modified for this purpose. The muscles of the abdominal wall not only support the abdominal viscera, and maintain them during their respiratory excursions, but also take a part in producing and regulating the movements of the body. Their functional value is often impaired in man, and hence he is the subject of those forms of slipping or dropping of the viscera which are grouped under the name of **viscerop-tosis**. He is liable to many other varieties of static disablements.

Inguinal and femoral hernia occur so rarely amongst mammals generally that they may be considered human peculiarities. Their frequency in

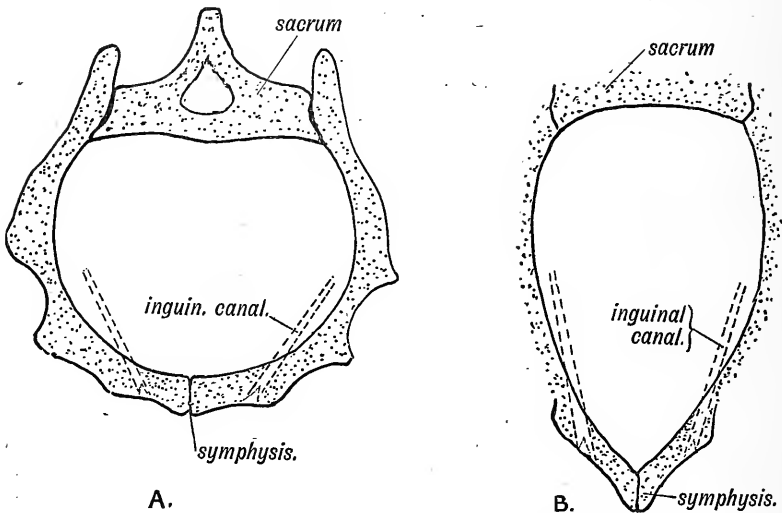


FIG. 428, A.—The Form of Pelvis and Inguinal Canal in Man.

B.—The corresponding forms in Pronograde Primates.

man is due to certain structural changes in his pubo-femoral region, changes which have resulted mainly from his adaptation to upright progression. His susceptibility to hernia is due to :

(1) The unique form of Poupart's ligament in man. It is scarcely developed in any other animal (Fig. 429). In the orang, for instance, also an upright primate, the external oblique has no attachment to the crest of the ilium, and takes no part in forming the outer part of Poupart's ligament (Fig. 429), the aponeurosis from the lower muscular digitations terminating directly in the pillars of the external abdominal ring, thus strengthening the region of the inguinal canal. This is the usual termination in the mammalia. In man the anterior part of the iliac crest has grown into the lower digitations of the external oblique and severed them from their tendinous fibres, which now form the main constituent of Poupart's ligament. The digitations thus inserted to the iliac crest help in balancing the body.

(2) The internal oblique and transversalis (conjoined parts) in the orang, and in all primates except man, arise from the firm tubular-sheath of the ilio-psoas, also from the extensive anterior border of the ilium, and, arching over the spermatic cord, end in a long insertion on the ilio-pectineal line. They act as a powerful compressor or sphincter of the inguinal canal, and thus prevent hernia (Fig. 429, *B*).

(3) The human manner of walking and the great head of the human child at birth require a wide pelvis. All mammals adapted to the pronograde posture have a narrow pelvis, and hence a narrow anterior abdominal wall (Figs. 428 *A* and *B*) through which the inguinal canal passes very obliquely. The course of the canal is more direct in man,

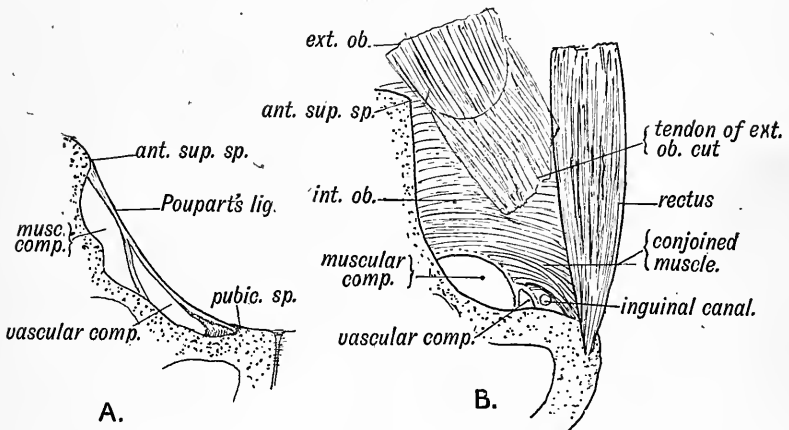


FIG. 429, *A*.—Poupart's Ligament and the Crural Passage of Man.

B.—Poupart's Ligament, Crural Passage, and Sphincter-like Conjoined Muscle of the Orang.

and therefore offers a greater facility to the escape of the abdominal contents.

(4) Owing to the width of his anterior abdominal wall, the size of the space between the edge of the pelvis and Poupart's ligament (the crural passage) is very much greater in man than in any other animal (Figs. 429 *A* and *B*). In him, the most internal part of the passage is left unfilled, and this unfilled space forms the femoral or crural canal through which femoral hernia may escape. The formation of the femoral canal has, therefore, no embryological basis; it is not like the inguinal canal the site of an embryological outgrowth of peritoneum. The crural passage is relatively larger in women than in men, owing to the greater size of the female pelvis, and hence femoral hernia is much more common in women than in men. Some hint as to the method of treatment of hernia in man may be obtained from a consideration of the arrangement of structures which prevent them in other animals.

(5) Perhaps the most important factor in the causation of hernia in man is the compression to which the abdominal contents are subjected by the contraction of the musculature of the abdominal parietes during

strenuous efforts, such as the lifting of heavy weights or the carrying of excessive burdens.

THE PELVIC FLOOR.

Coccyx.—The retrograde changes undergone by the coccyx in the evolution of the human body are intimately connected with the formation of the pelvic floor. The coccyx in man is commonly composed of four vertebrae, more or less vestigial in nature, which represent the basal caudal vertebrae of tailed mammals. Evidence of their vestigial or retrograde nature is to be found in :

(1) Only their centra are developed—with the exception of the first, which shows partial formation of transverse processes and neural arches (superior cornua) ;

(2) Delay in the appearance of the centres of ossification. These, instead of beginning in the 8th week as in a typical vertebra, commence after birth. The centre for the 1st coccygeal vertebra appears in the 1st year, that for the 4th vertebra about the 25th year ; the 2nd and 3rd at intermediate periods. All four are fused into one piece about the 30th year.

(3) Late in life, between the 40th and 60th year, the coccyx unites with the sacrum.

The number of coccygeal vertebrae varies ; four is the normal number, but there may be three or five. In the 7th week embryo as many as eleven coccygeal vertebrae have been counted. The first coccygeal vertebra may join the sacrum, making six sacral vertebrae. The coccygeal vertebrae in anthropoids are more reduced as regards the development of their parts than in man.

The evidence of the former existence of a **true tail** in the ancestral human stock consists of :

(1) From the 5th to the 8th week the coccygeal region of the spine protrudes (Fig. 430), and the vertebrae number from 8 to 11 ; the notochord is traceable beyond the vertebral segments.

(2) Vestiges of the extensor and flexor muscles of the tail are frequently found (10 % of bodies) on the dorsal and ventral aspects of the sacrum and coccyx. Occasionally small nodules of bone are found in front of the human coccyx, spanning the continuation of the middle sacral (caudal) artery ; these nodules represent the chevron bones or haemal arches of tailed mammals. The depressors of the tail are attached to the chevron bones (see Fig. 431).

(3) True tails, consisting of external prolongations of the coccygeal region, commonly fibrous, rarely containing vertebrae, occasionally occur.

(4) The post-anal pit, always to be seen in the newly born child, marks the point at which the coccyx disappears below the surface early in the 3rd month. In man the coccyx forms part of the perineal floor. Instead of projecting far beyond the gut, as in tailed mammals, it terminates $1\frac{1}{4}$ inches above the commencement of the anal canal.

Pelvic Floor is peculiarly extensive in man, an adaptation to his upright posture. The floor is formed by the following structures :

(1) The levator ani and its sheath (recto-vesical and anal fasciae) on each side ; (2) The coccyx and coccygeus muscles ; (3) The constrictor urethrae and triangular ligament ; (4) The pyriformis and its sheath may also be included.

Development of the Pelvic Floor.¹—The pelvic floor has been evolved in man by a transformation of the tail and the caudal muscles. The arrangement of tail muscles in a four-footed mammal, such as the monkey or dog, is shown in Fig. 431, *A*, and the modification of this form in anthropoids and man in Fig. 431, *B*. In mammals, two muscles, the pubo-

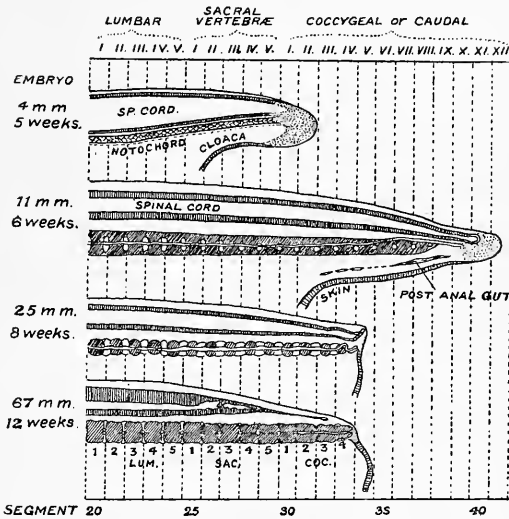


FIG. 430.—The rise and retrogression of the caudal vertebrae during the 2nd month of development. (After Kunitomo.)

coccygeus and ilio-coccygeus act as depressors of the tail, which in four-footed animals plays the part of a perineal shutter ; in orthograde primates the tail no longer helps to close the perineum, its muscles being required for the support of the pelvic viscera. In pronograde apes these muscles are attached to the small V-shaped chevron bones on the under surface of the basal caudal vertebrae (Fig. 432). Another muscle, the ischio- or spino-coccygeus, acts as a lateral flexor of the tail. It is attached to the transverse processes of the caudal vertebrae, and rises from the dorsal border of the ischium. In man the pubo-coccygeus and

¹ The following are some of the British papers dealing with this subject : P. Thompson, *Myology of the Pelvic Floor*, Manchester, 1899 ; R. H. Paramore, *Lancet*, 1910, May 21st and 28th. In the *Journal of Anatomy and Physiology* the following papers have appeared : P. Thompson, 1901, vol. 35, p. 127 ; A. M. Paterson, 1907, vol. 41, p. 93 ; D. Derry, 1908, vol. 42, p. 97 ; G. Elliot Smith, 1908, vol. 42, p. 198 *et seq.* ; J. Cameron, 1908, vol. 42, p. 438.

ilio-coccygeus are blended into one sheet and form the levator ani. The shrinkage of the tail leaves the muscle partly stranded on the ano-coccygeal ligament (Fig. 431, *B*). Other fibres of the pubo-coccygeus lose their primary insertion to the coccyx, and become attached to the prostate, central point of the perineum, and to the anal canal. Both muscles, especially the ilio-coccygeus, retain in part their primitive attachment to the coccyx (*cauda*). The spino-coccygeus, or coccygeus muscle, is partly fibrous in man, its outer laminae forming the small sacro-sciatic ligament; its inner laminae remain muscular and form the coccygeus. In man,

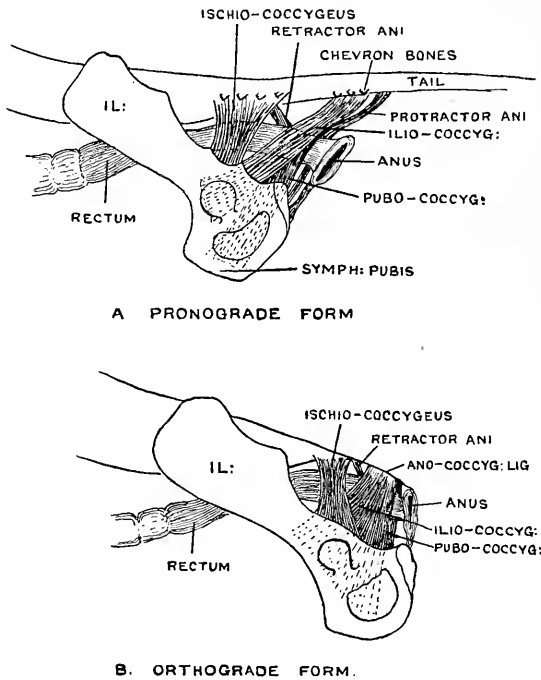


FIG. 431.—Diagram to show the Pelvic Muscles of a Pronograde Ape (*A*) and of an Orthograde Ape (*B*).

too, the origin of the ilio-coccygeus has sunk from the pelvic brim of the ilium on to the obturator fascia (P. Thompson); traces of the primitive origin from the pelvic brim can often be detected (Fig. 433). The white line, a structure peculiar to man, marks the new point of origin of the levator ani from the obturator fascia.

In fishes (selachians) the levator ani is represented by a backward continuation of the rectus abdominis (Paramore). The pelvic part of the rectus is attached behind to the tail; anteriorly it is attached to the movable pelvic girdle. The cloaca of the dog-fish passes out between the right and left primitive representatives of the levator ani, which can compress the cloaca, not by depressing the tail as in mammals, but by pulling the pelvis backwards.

Pelvic Fascia and Fasciae in General.—It has been customary to regard fasciae as separate structures forming distinct sheets with devious

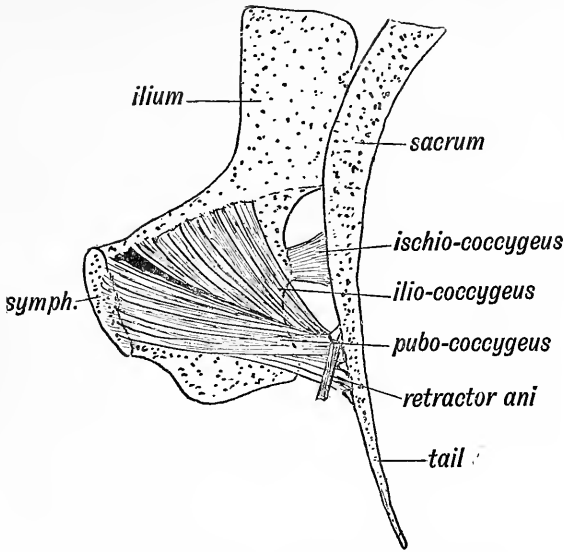


FIG. 432.—The Pelvic-caudal Muscles of a Monkey.

and complex courses. It is possible by dissection to prepare and display them according to accepted descriptions, but the structures so displayed

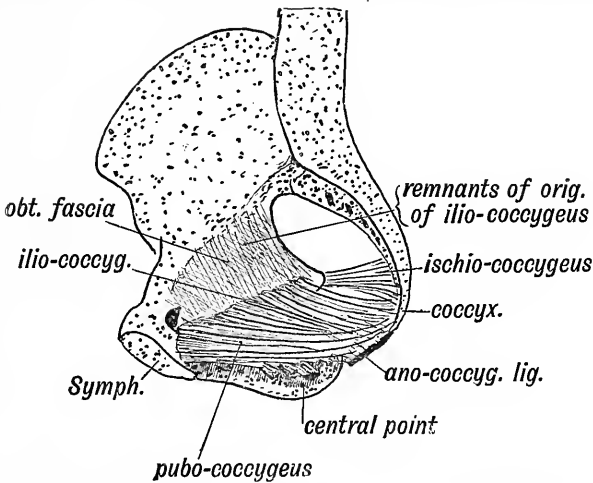


FIG. 433.—The Pelvic Muscles of Man—corresponding to those shown in Fig. 432.

are artificial and not the true structures which the surgeon or physician has to deal with in actual practice. Embryology is the best guide to their

nature. Take, for example, the development of the fasciae seen on making a section of the upper arm (Fig. 434). When the limb bud has appeared, which it begins to do about the end of the 4th week of development, a section through it reveals a syncytium of mesodermal cells, the blastema of bones, muscles, etc., surrounded by a covering of ectoderm (Fig. 435). Very soon the central cells near the axis of the bud are densely grouped and form the basis of the skeletal axis. Others, derived from extensions of the primary muscle plates (Fig. 435), arrange themselves to form the biceps, triceps and muscles of the arm; others become the walls of vessels and the sheaths of nerves. After these various groups of cells have become differentiated, there is left over a cellular residue in which the highly differentiated cell-groups are enmeshed. The undifferentiated mesoderm

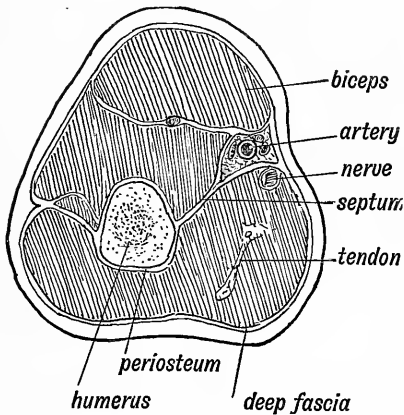


FIG. 434.—Section across the Upper Arm to show the continuity of its Fascial System.

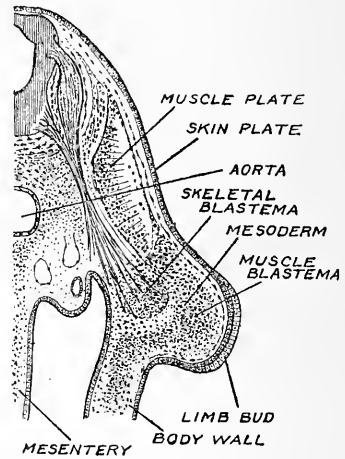


FIG. 435.—Section of a Limb-bud to show the manner in which its tissues become differentiated. (After Kollmann.)

forms the connective tissue or fascial system of the part. From the manner of its origin it is evident that the connective tissue system—the fasciae and septa—must form a continuous sponge-work of sheaths, each being in continuity with that of every surrounding structure. The sheaths of the biceps, triceps and brachialis anticus, the periosteum of the humerus, the deep fascia, internal and external intermuscular septa, the sheaths of the vessels and nerves of the arm, represent the mesodermal tissue which was left over after the individual structure of the brachium were differentiated, and are, from the manner of their origin, necessarily in continuity (Fig. 434). They can only be artificially separated from each other. It is more accurate and easier to describe fasciae, then, not as separate structures, but as adjuncts of the structures which they surround or ensheath. As to the manner in which **connective tissue** is developed, there are two opinions: (1) that the substance of the cell body elongates and forms a fibre; (2) the more probable, that fibres are formed in a

substance which lies outside the cell body, but is under the influence of the cell.¹

The Pelvic Fascia, which strengthens the pelvic floor, is composed of the sheaths of four muscles :

(1) Levator Ani ; (2) Obturator Internus ; (3) Piriformis ; (4) Constrictor Urethrae and deep Transversus Perinei.

The fibrous capsules of the following viscera also form part of it :

(1) Prostate and Vesiculae Seminales in the male ; (2) Vagina and Uterus in the female ; (3) Bladder ; (4) Rectum. Under the title of pelvic fascia these eight elements are combined. To these must be added the important sheaths of the vessels—especially of the vesical, uterine and perineal arteries.²

I. The **Obturator Fascia** is the sheath on the inner or pelvic aspect of the obturator internus ; the sheath on the outer side of the muscle is formed by the periosteum and obturator membrane. The obturator fascia is attached at the circumference of the muscle. There it becomes continuous with the periosteum of the os innominatum. The part above the white line (supra-linear) is intra-pelvic ; the part below (infra-linear) is perineal and situated on the outer wall of the ischio-rectal fossa.

II. **Recto-vesical and Anal Fasciae.**—The levatores ani form a muscular floor for the pelvis, stretching from the white line of one side to the white line of the other. The sheath on their under surface—on the inner wall of the ischio-rectal fossa—forms the anal fascia. On the upper surface, their sheath forms the greater part of the recto-vesical fascia. The pelvic viscera rest on the upper surface of the levatores ani and the capsules of the viscera are continuous with the sheath on the upper surface of the muscles. The combined visceral capsules and upper sheath of the levatores ani form the recto-vesical fascia.

III. The **Triangular Ligament** is situated in the neighbourhood of the constrictor urethrae muscle (Fig. 436), but it can scarcely be regarded as its sheath. It is rather a fibrous septum for giving attachment to the prostate on its deep or pelvic surface and to the bulb and root of the penis on its lower or perineal aspect (Delbet, Elliot Smith). The inferior transverse fibres of the constrictor form really a separate muscle—the deep transverse perineal. The apex of the prostate rests on the muscle, its fibrous capsule being continuous with the posterior layer of the muscle sheath—the deep layer of the triangular ligament.

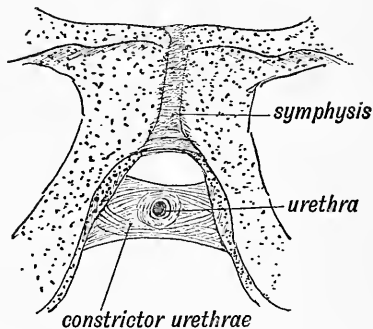


FIG. 436.—The Constrictor Urethrae Muscle.

¹ For literature see F. P. Mall, *Amer. Journ. Anat.* 1901, vol. 1, p. 329 ; A. von Szily, *Anat. Hefte*, 1907, vol. 33, p. 225 ; J. S. Ferguson, *Amer. Journ. Anat.* 1912, vol. 13, p. 129 ; Korff, *Ergebnisse der Anat.* 1907, vol. 17, p. 247.

² See references on p. 409 under the names of Prof. A. M. Paterson and Prof. Elliot Smith.

IV. The inner sheath of the pyriformis forms the **pyriform fascia**. The coccygeus is continuous with the levator ani and its sheath forms part of the recto-vesical fascia. The loose perirectal sheath is also continuous with the tissue of the fascia pyriformis.

The pubo-prostatic ligaments and the lateral vesical ligaments are strengthened parts of the fibrous capsule of the prostate, which provide the bladder with a pubic fixation. The vesical musculature, in emptying the bladder, acts from the pubic fixation thus obtained. The great strains to which the pelvic vessels are exposed when the pelvic floor and viscera are depressed in forced muscular efforts renders a strong fibrous protective sheath necessary. Hence the tough fibrous coating round the uterine and vesical vessels. Alcock's canal is formed from the fibrous sheath round the pudic artery and nerve (Elliot Smith).

Cervical Fascia.¹—From what has been said of the pelvic fascia, the nature and arrangement of the cervical fascia will be readily understood. It is composed of (1) the sheaths of the cervical muscles (sterno-mastoid, etc.); (2) of the sheaths of vessels (carotid sheath, etc.); (3) the sheaths of nerves (axillary sheath, etc.); (4) the fascial capsules of viscera, such as the thyroid body, salivary glands, and pharynx. The carotid sheath and sheaths of the great vessels from the base of the skull to the pericardium within the thorax are formed to a great extent from mesodermal tissue which was developed within the visceral arches of the pharynx. At first the pericardium lies beneath the mouth and pharynx. With the development of the neck at the end of the 2nd month of foetal life, the cervical structures and their sheaths become stretched, but they maintain the ancient connection between skull base and pericardium.

The muscular sheaths on the inner aspect of the transversalis, iliacus and psoas also have been regarded as forming distinct fasciae.

On the other hand, some fasciae are quite discrete structures. The palmar fascia is part of the palmaris longus muscle; the plantar, part of the plantaris muscle; the vertebral aponeurosis or fascia, part of the layer of muscle which is represented by the serratus posticus superior and inferior; the epicranial aponeurosis is part of the platysma sheet. The middle layer of the lumbar fascia represents a primary septum developed between the dorsal and ventro-lateral groups of musculature (see p. 68).

Fascial structures have also a distinct relationship to the **lymphatic system**. Lymphatics follow the septa and capsules of glands and muscles; the lymphatics of the lung collect in the connective tissue separating its lobules. The most remarkable of all the capsular tissues of the body are those represented by the membranes of the central nervous system; there the cerebro-spinal spaces, or clefts, have separated the cerebral capsule into three layers—the pia mater, arachnoid and dura mater.

Leonard Hill has also drawn attention to the part which ensheathing fasciae play in assisting the circulation of the blood. Every contraction of the muscles of the thigh tends to force the venous blood within the sleeve formed by the fascia lata on towards the heart.

¹ See Prof. F. G. Parsons, *Journ. Anat. and Physiol.* 1910, vol, 44, p. 153.

Body Wall.—Having thus traced the evolution of the pelvic floor and discussed the nature of fasciae generally in connection with the pelvic fascia, we pass on to consider the development and nature of the abdominal and thoracic walls.

Bilateral Symmetry of the Body.—From a developmental point of view the body is made up of two symmetrical halves; each half of the embryonic plate, taking the medullary groove as the line of division, contributes equally to the formation of the body. Each produces a half of the nervous system, each a half of the vascular, muscular and alimentary systems, so that each individual is in reality made up of two identical halves,

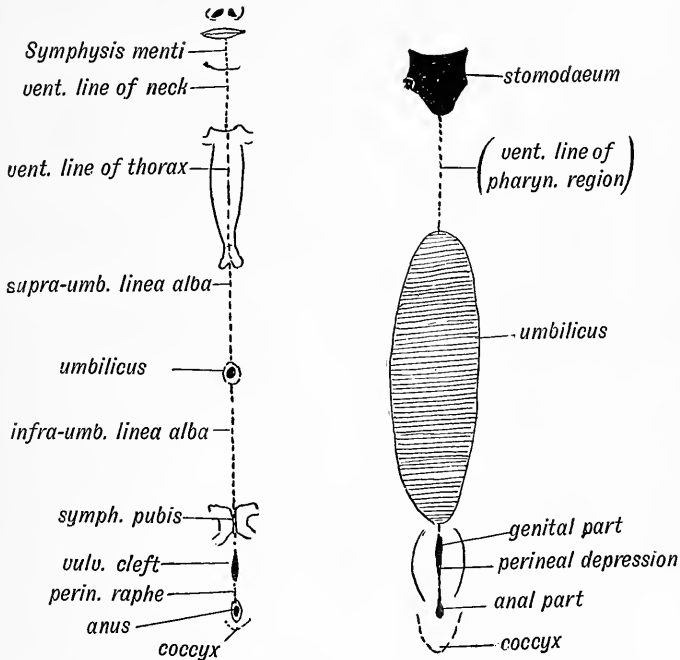


FIG. 437.—Diagram of the Structures formed in the Median Ventral Line of the Body.
 FIG. 438.—The Median Ventral Line in an Embryo of 4 weeks, to contrast with the Corresponding Line in the Adult.

right and left. Although each side of the body rises from the same blastocyst, yet each becomes specialized structurally and functionally so that, as development goes on, there appears a very remarkable asymmetry.

Ventral Line of the Body.—The structures within the right and left body walls become united along the **ventral line** from the mouth to the anus (see Fig. 437). The mesoderm, muscle plates, dermatomes, nerves and cartilaginous outgrowths, which are produced on each side of the median dorsal line of the body, meet on each side of the median ventral line. In this line are developed the symphysis of the lower jaw, the body of the hyoid bone (copula), the white line of the neck and angle of the thyroid cartilage, the sternum, the supra-umbilical part of the linea alba, umbilicus,

infra-umbilical part of the linea alba, symphysis pubis, the septum of the penis, and of the scrotum and perineal raphe. The ventral line is continued forwards on the face between the parts derived from the mesial nasal processes.

The idea was at one time prevalent that the whole of this line was formed by the fusion of one somatopleure with the other; the median ventral line was the suture formed by the union. Such is not the case. The blastoderm, which lies at first like a cap on the yolk sac (Fig. 18), is produced or folded anteriorly to form the fore-gut and the part of the body above the umbilicus; it is produced posteriorly to form the hind-gut and the part of the body below the umbilicus. The blastoderm grows out from the

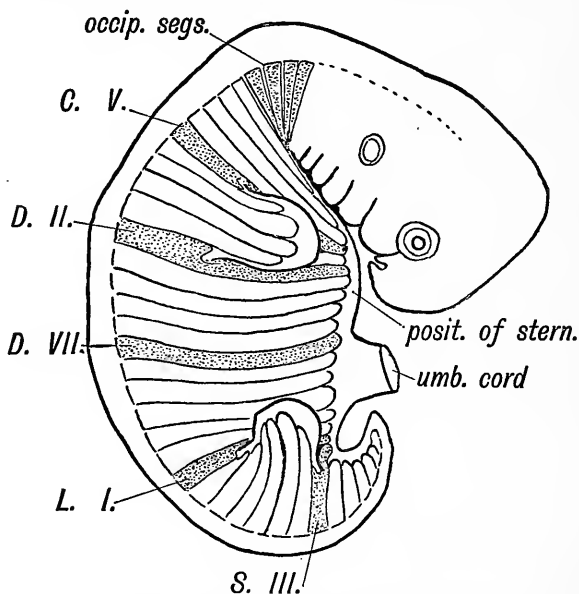


FIG. 439.—Diagram of a Human Embryo (6th week) showing the Arrangement and Extension of the Mesoblastic Segments. (After A. M. Paterson.) The first and last of each segment entering into the formation of the limbs is stippled. The position is indicated in which the sternum is formed.

umbilicus to form the embryo in much the same way as a soap-bubble is blown from the bowl of a pipe. In an embryo, at the commencement of the 4th week, the greater part of the ventral line is occupied by the umbilicus (Fig. 438). At that time the umbilicus is 3 mm. long, the entire ventral line being about 4 mm. At the end of the 7th week the ventral line measures 15 mm., the umbilicus retains its former size, about 3 mm.

At first the somatopleure shows no trace of segmentation. The paraxial masses of mesoderm become segmented early and form the muscle plates (Fig. 65). From each muscle plate of the primitive segments a process grows down into the somatopleure (Fig. 439). The somatopleure thus becomes segmented secondarily, the process of segmentation spreading from the dorsal to the ventral side of the plate, but along the median

ventral line of the body wall, a band of the primitive mesodermal tissue remains unchanged and undifferentiated. In the ventral band between the left somatopleure and the right are formed the sternum and the linea alba (Fig. 437). In lower vertebrates, in fishes, and to a less marked extent in amphibians and reptiles, the myotomic segments remain distinct from end to end of the trunk.

Formation of Ribs.¹—Ribs, like all true skeletal bones, pass through three stages : (1) They are represented by a mesenchymatous or membranous basis in the fibrous tissue (septa) between the muscular segments of the somatopleure (Fig. 439). The condensation of the costal mesenchyme appears at the beginning of the 5th week as a separate vertebral element. (2) The mesenchymatous basis or **blastema** of the rib becomes cartilaginous. (3) Ossification of the cartilage begins in the 8th week, but the process of ossification leaves the ventral parts of the costal segments untouched ; they form the costal cartilages ; in lower forms they become ossified and form sternal ribs. The process of chondrification begins at the dorsal end of the ribs in the 6th week, and spreads ventrally, thus repeating the order in which the blastema was laid down. The extension ventralwards of the ribs corresponds with the growth and expansion of the lungs ; at the beginning of the 7th week they scarcely reach the lateral or axillary line of the body, but by the end of this week they have effected a junction with the sternal bars (Fig. 443). The ribs from the 1st to the 7th are developed in the somatopleure over the pericardium. In lower vertebrates, such as reptiles, each rib articulates with the neural arch of a vertebra by two heads, dorsal and ventral (Fig. 60). The tuberosity of a rib represents its dorsal head. In man, with the exception of the first and last rib, or in some cases, the two last ribs, the costal head is placed opposite an intervertebral disc, for in position the disc represents the ventral or chordal part of a primitive vertebra. In the case of the first rib the head has shifted backwards to the body of the first vertebra, while in the 12th and sometimes the 11th, the head and tuberosity are fused, and both articulate with the part of the vertebra which represents a transverse process.

The Sternum.—In man and anthropoids the sternum has become flat and highly modified with the alterations in the shape of the thorax (Fig. 372). With the adaptation to the upright posture the thorax becomes flattened from back to front ; its transverse diameter is as great, or greater, than the antero-posterior. The type of respiration is greatly altered. The sternum also becomes wider and shorter. To understand the nature of this change, it is necessary to note the characters of the sternum of a pronograde mammal, such as the dog or ape (Fig. 440). In such, the sternum is typically made up of seven segments :

1. A modified anterior segment, the **pre-sternum** ;
2. Five narrow, cylindrical segments or *sternabrae*, forming the **body** of the sternum ;
3. The **ensiform process**, a hind segment, complex in nature and ending in the

¹ For development and differentiation of ribs see Charles R. Bardeen, *Amer. Journ. Anat.* 1905, vol. 4, p. 163 ; also p. 265 ; Geddes, *Journ. Anat. and Physiol.* 1913, vol. 47, p. 18. For ossification of ribs : Franklin P. Mall, *Amer. Journ. Anat.* 1906, vol. 5, p. 433.

middle ventral line. The ensiform process frequently bifurcates and is never segmented.

The chief changes in the human sternum are :

1. Each segment has become flat and wide ; 2. The segments of the body fuse together during the years of adolescence, the fusion beginning behind and passing forwards ; 3. The 4th sternabra of the body is usually vestigial and is probably made up of two or more fused segments.

In low primates 8 or 9 pairs of ribs may reach the sternum, six or more sternabrae being then present. In man the number has been reduced to 7 pairs, the sternal ends of the 7th pair lying in front of the fourth sternabra. It is not uncommon to find the 8th rib reaching the sternum, especially

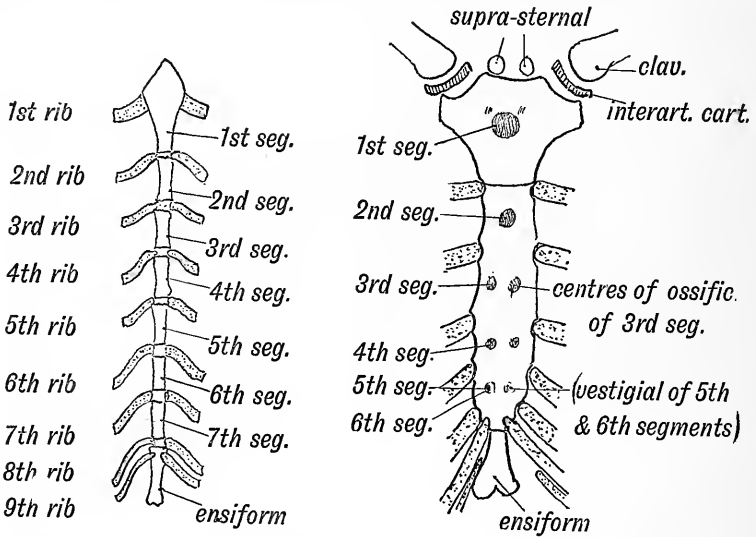


FIG. 440.—The Form of Sternum in a Pronograde (quadrupedal) Mammal.

FIG. 441.—The Form of Sternum in a Mammal adapted to the Orthograde (upright) Posture. The Points of Ossification are also shown.

on the right side ; it is rare to find the 7th pair fail to reach the sternum. The more frequent presence of an 8th sternal rib on the right side is due to right-handedness (Cunningham), or, as seems more probable, to give a more secure origin to the right costal fibres of the diaphragm, which have a greater resistance to overcome during inspiration, than those of the left side. In man and the anthropoid apes a new feature appears in the lower costal cartilages. The 5th, 6th and sometimes the 7th throw out processes which articulate with the cartilage below. When, during inspiration, the diaphragm raises the chest, these articulations permit it to elevate the 5th and 6th pairs of ribs as well as the 7th pair.

Morphology of the Sternum.¹—In amphibia the ventral parts of the shoulder and pelvic girdles develop towards the ventral median line. In

¹ The account given by Paterson (Hunterian Lectures, 1903) has been followed with some modifications. For an introduction to the more recent literature see

the median line a rod of cartilage is formed between them (Fig. 442). The median rod is differentiated as right and left bars from the ventral parts of the limb girdles. The right and left bars fuse to form the median cartilage. The median rod between the shoulder girdles becomes the sternum; it is divided into three parts—anterior, which projects in front of the girdle (omo-sternum or supra-sternum); posterior, behind the girdle; and the middle, with which the shoulder girdle articulates (Fig. 442, *A*). The sternum affords a basis from which muscles act on the shoulder girdle, and also a ventral basis for the articulation of the shoulder girdle. In all classes of vertebrates, the sternum is developed over and shields the heart. The median cartilage of the pelvic girdle is similarly divided into anterior, middle and posterior parts (Fig. 442, *B*).

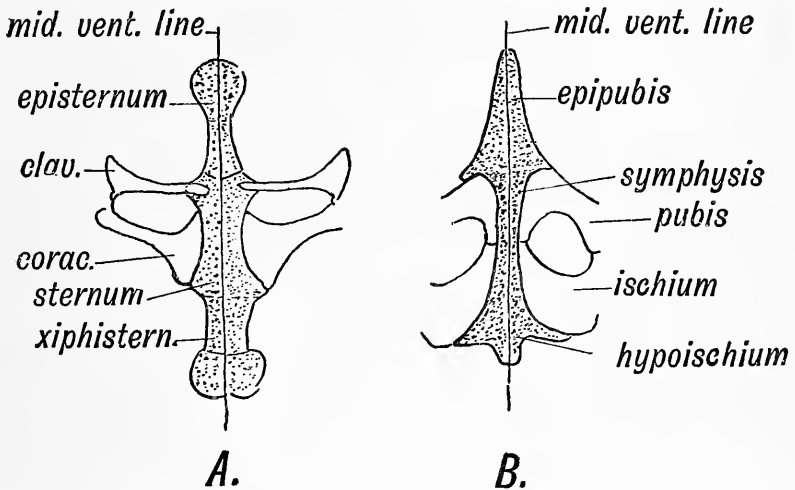


FIG. 442.—The Cartilages developed on each side of the Median Line between the Shoulder and Pelvic Girdles. *A*, the shoulder girdle of the frog; *B*, the pelvic girdle of sphenodon. (The term "epi-sternum" is wrongly applied in Fig. *A*; it should be omo-sternum or supra-sternum. There is now a general agreement that the term epi-sternum should be applied to the membrane bone formed between the clavicles.)

The evolution of a costal type of respiration in reptiles leads to a further stage of development. Some of the costal processes of the vertebrae grow towards the median ventral line, some of them reaching and articulating with the middle part of the bar between the shoulder girdles; this part now serves as a fulcrum or sternum for both ribs and girdle. Such a condition is also seen in birds and monotremes (Fig. 466). In the higher mammals, the ventral part of the shoulder girdle retains only its ventral connection with the sternum through the clavicle; it still serves as the basis of origin for muscles which act on the shoulder girdle and on the arm. Its chief purpose has become respiratory. In the human sternum the three parts of the primitive sternum can be recognized: the supra-sternal bones (Fig. 441), which are only rarely separated from the presternum, represent

the anterior part (omo-sternum); the manubrium and body, the middle part of the shoulder girdle sternum; and the ensiform process, the posterior part.

Development of the Sternum.—In Fig. 443 four stages in the development of the human sternum are represented. Stage *A* shows the extent to which the ribs have become chondrified at the end of the 6th week; the cellular costal blastema, into which the process of chondrification is spreading, is not shown. In the following week (Stage *B*) the process of chondrification has reached the middle line in the region of the presternum.

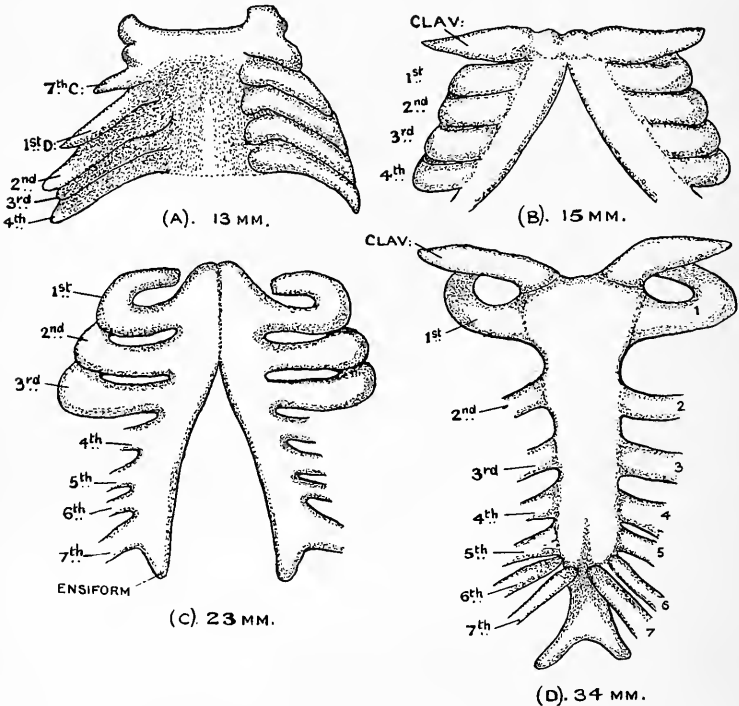


FIG. 443.—Four Stages in the Chondrification of the Human Ribs and Sternum and showing the Fusion of the Sternal Bars. (After Charlotte Müller.) *A*, end of 6th week; *B*, end of 7th week; *C*, end of 8th week; *D*, end of 10th week.

The ventral ends of the ribs are now joined together by a ventral or lateral sternal bar. The sternal bars in the region of the presternum have begun to fuse together across the middle line. At their anterior extremities they are joined by the ventral cartilaginous end of the clavicle. In the presternum there is thus an element apparently derived from the ventral end of the clavicle. In Stage *C*, about the end of the 8th week, the process of fusion is advanced, but the projection of the foetal heart and liver at this time (see Fig. 45), tends to keep them apart. Each sternal bar has now 7 ribs continuous with it, and its posterior end is free. Early in the 3rd month (Stage *D*) the process of fusion is complete, the cartilaginous basis of the sternum has been formed by the fusion of right and left bars.

At the end of the 2nd month the diaphragm is descending to its final position, the pleural cavities are rapidly forming, and the liver is assuming a more abdominal position. Charlotte Müller,¹ whose illustrations are represented here, found that the mesenchymal sternal bars were chondrified as direct extensions from the ribs.

The sternum is thus developed in the median ventral line over the pericardium and between the mandible in front and the umbilicus behind (Figs. 437, 439). The mesoderm condenses during the 5th week on each side of this part of the median line to form the right and left mesenchymal halves of the sternum, which anteriorly are continuous with the bases of the ventral part of the shoulder girdle (Fig. 444). These two halves, the right and left **mesenchymal sternal bars**, fuse gradually in the middle

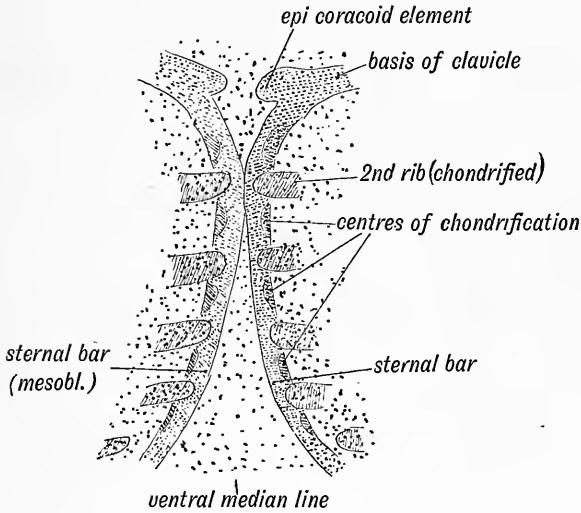


FIG. 444.—The Sternal Bars in an Embryo of 7 weeks. (After Paterson.)

line, the process of fusion commencing at the presternum and spreading backwards.

The sternum is regarded by Paterson as a structure rising independently of the ribs on each side of the median ventral line. This, however, is not the commonly accepted view. Ruge's researches led him to the conclusion that the segments of the sternal bars were produced as buds from the ventral ends of the ribs. The evidence of comparative anatomy and the difference in the type of the cartilage cells in the costal and sternal elements negative Ruge's interpretation.

In its development the sternum passes through three stages—fibrous, cartilaginous and bony.

1. **Fibrous or mesenchymal Stage.**—In the 7th week (Fig. 444) the costal cartilages are already chondrified. The mesoderm on each side of the median line, in which they end, has become condensed, and forms

¹ *Morph. Jahrb.* 1906, vol. 35, p. 591.

the membranous basis of the two sternal bars (Paterson). The bars begin to fuse together anteriorly.

2. **Cartilaginous Stage.**—The blastema of each sternal bar begins to chondrify in the intervals between the ends of the costal cartilages. The process of chondrification and fusion proceed apace, and by the commencement of the third month the segments of each side have united to form the **cartilaginous** sternal bars (Paterson). Fibrous joints are subsequently formed between the presternum and mesosternum and between the mesosternum and ensiform process. A fibrous, and then synovial joint, is also developed at the union of the costal cartilages with the sternum, except in the case of the first pair, where a synovial joint is only occasionally present.

3. **Ossification.**—A centre appears for each sternabra; those for the third and fourth of the mesosternum are frequently double, one being placed on each side. The centres for the 4th mesosternal segment are frequently absent. The centre for the presternum (there may be two or even more) appears about the 4th month; the centres behind appear in the 6th and 7th month; that for the 4th sternabra of the mesosternum appearing about the time of birth; that for the ensiform four or five years after birth. The process of fusion of segments begins behind about puberty; the segments of the mesosternum are united together by the 25th year. Occasionally a median foramen may be seen in the sternum; it is due to imperfect union of the sternal bars.

Sterno-Manubrial Joint¹ becomes of great functional importance in man and those primates adapted to the upright posture. Even in old age this joint is rarely ossified (8 per cent., Paterson). In man a considerable respiratory movement occurs between the manubrium and body of the sternum. The manubrium moves in continuity with the ventral ends of the first pair of ribs; the body of the sternum follows the excursion of the 3rd to the 7th pairs of sternal ribs. As a rare abnormality (commoner in black than in white races) this joint is formed between the first and second segments of the mesosternum.

Presternum.—Clear evidence of the origin of the sternum from the shoulder girdle is to be seen in the presternum. In the earlier developmental phases, it is continuous with the precoracoid element in the ventral end of the clavicle (Figs. 442, 443, 444). It is separated from this element by the development of the sterno-clavicular joints and meniscus. In over 80 per cent. of bodies the upper border of the human manubrium sterni shows traces of the supra-sternal bones which represent the anterior parts (omosternum, epicoracoids) of the primitive sternum. Very rarely these bones are separate (Fig. 441); commonly they are present as elevations or nodules on each side of the suprasternal notch (Paterson). The interclavicular ligament, which represents the interclavicle of birds (episternum), reptiles and monotremes (Fig. 466), is attached to the presternum.

¹ Keith, *Further Advances in Physiology*, edited by Leonard Hill, 1909 (Arnold); *Journ. Anat. and Physiol.* 1896, vol. 30, p. 275.

Linea Alba.—The separation of the sternal bars is not a reproduction of an ancestral phase, but is simply due to an embryological convenience to accommodate, first the yolk sac and later the large heart and liver of the embryo. In Fig. 445 is shown the early condition of the linea alba—from the classical research by Bardeen and Lewis.¹ The umbilical cord is still distended by a loop of intestine, and the two recti are wide apart, separated by the mesial ventral membrane—the **primitive linea alba**. The two sternal bars are also held apart by the condition of the umbilical structures; indeed, the primitive linea alba is not only wide, but also extends from the neck to the perineum. In the 10th week the intestines

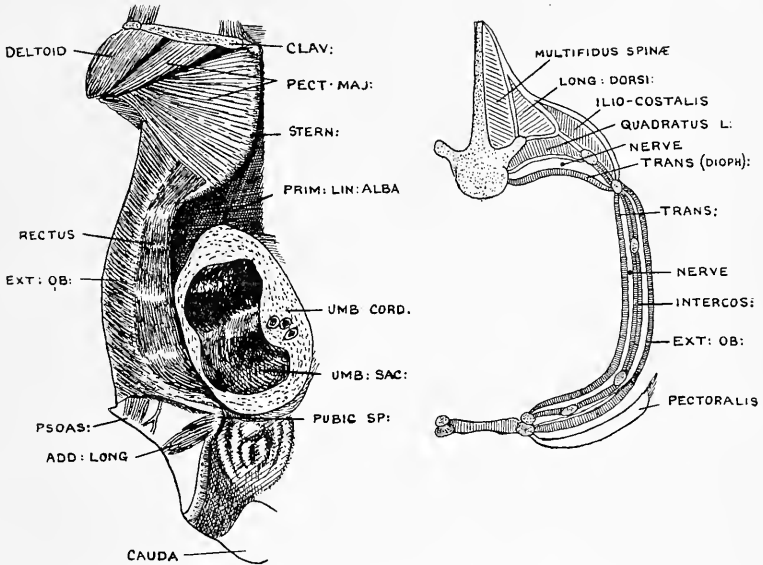


FIG. 445.—The Primitive Linea Alba in a Human Foetus in the 8th week—20 mm. long. (After Bardeen and Lewis.) Only the right half of the body is shown; the rectus abdominis is lateral in position, it and the sternal bars being kept from the mesial ventral line by the structures in the neighbourhood of the umbilicus.

FIG. 446.—Transverse Section of the Thoracic Wall of a Lizard to show the Primitive Arrangement of the Muscular Strata of the Body Wall.

return from the umbilical cord to the abdomen, the chest wall expands before the growing lungs and the mesial ventral line becomes gradually closed.

In Fig. 446 a transverse section is shown of the muscular layers in the anterior or thoracic body cavity of a lizard, and which also represents a stage in the evolution of the musculature of man's body wall.² It will be seen that there are three layers: an outer represented by the rectus and

¹ C. R. Bardeen and W. H. Lewis, *Amer. Journ. Anat.* 1901, vol. 1, p. 1; *Amer. Journ. Anat.* 1901, vol. 1, p. 145 (Nerves of Abdominal Wall).

² Keith, *Journ. Anat. and Physiol.* 1905, vol. 39, p. 243; Kazzander, *Anat. Hefte*, 1904, vol. 23, p. 541 (Dev. of Rectus Abdominis):

external oblique; an inner by the transversalis, and a middle double layer—the internal and external intercostals. In the abdomen they are combined in one layer—the internal oblique. The three layers are functionally different; the transversalis is a constrictor of the body cavity; the middle layer is mainly respiratory in its action; the outer is also respiratory, but chiefly concerned in body movements.

CHAPTER XXVI.

DEVELOPMENT AND DIFFERENTIATION OF THE LIMB BUDS.

Evolution of the Limbs.¹—The nature of the primitive structures from which limbs were evolved is still a much debated question. The manner of their development in vertebrate embryos makes it certain that they were not outgrowths from the vertebral system; in every case they sprout out from the somatopleure, which encloses the body cavity, and are always supplied by the nerves of that lamina—the ventral branches of the spinal nerves. We are also certain that the limbs correspond to the pectoral and pelvic fins of fishes. It is clear that when land-living vertebrates were evolved, the slight structures which were equal to the balancing and finer movements of an animal suspended in water, had to undergo great modifications in order to become capable of moving and supporting the body on a solid medium. It was with the evolution of pulmoniferous land-living vertebrates that a very definite type of limb made its appearance. In all cases the limb of a primitive Tetrapod is built on the same plan; it is made up of a basal segment or girdle, with a free part divided into proximal, middle and distal segments. The distal segment carried 5 digits.

Although man has departed greatly from the primitive mammalian type in the structure of his brain and trunk, yet in the elements which enter into the formation of his limbs he has retained more of the ancestral mammalian features than many other mammals. He retains the original number of digits; the bones of his hand and foot are much less specialized than those of the horse. It is true that the skeleton of his lower extremity has been extensively modified for his plantigrade posture, yet under all the adaptational features one can see very clearly the outlines of a most primitive form. He comes of a stock which led an arboreal existence almost from the dawn of the mammalian type.

Embryonic Limbs.²—The limbs begin to appear at the end of the 4th week. A slight elevation or ridge is then seen to run along the dorsal

¹ The following papers will give those interested a clue to the extensive literature on this subject: Osburn, *Amer. Journ. Anat.* 1907, vol. 7, p. 171; Goodrich, *Quart. Journ. Mic. Science*, 1906, vol. 50, p. 333; E. Müller, *Anat. Hefte*, 1909, vol. 39, p. 469; D. M. S. Watson, *Journ. Anat.* 1918, vol. 52, p. 1; W. K. Gregory, *Annals N. Y. Acad. Sc.* 1915, vol. 26, p. 317; Prof. Wood Jones, *Arboreal Man*, 1915; *Principles of Anatomy*, 1920.

² Development and Differentiation, see Bardeen's Monographs, *Amer. Journ. Anat.* 1905, vol. 4, pp. 163, 265; vol. 6, p. 259 (muscles and nerves of lower extremity);

border of the somatopleure, at some distance from the row of primitive segments formed in the paraxial mesoblast (Fig. 447). The limb buds spring from this ridge as flat processes with an upper, dorsal or extensor surface, and a lower, ventral or flexor surface. The two borders are anterior or cephalic and posterior or caudal. It is generally held that the lateral ridge, of which the limb buds are specialized parts, represents a continuous row of lateral fins. If this view is right, then the fore and hind limbs represent highly specialized fin-rays.

A section shows each bud to be composed of undifferentiated mesoderm, with a covering of ectoderm (Figs. 435, 454). It represents in structure a process of the undifferentiated mesoderm of the somatopleure or body wall; hence the limbs are to be regarded, not as structures developed from the axis of the embryo, but as *processes of the body wall*. Extensions

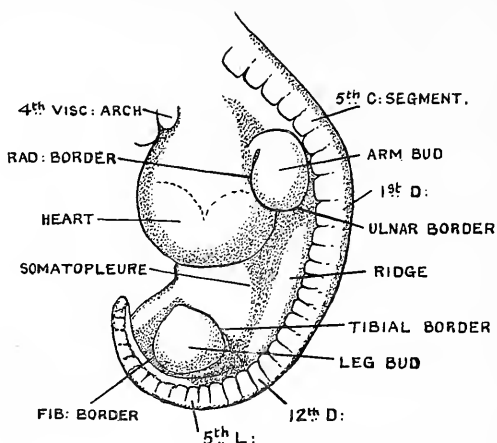


FIG. 447.—Lateral View of a Human Embryo at the 28th day, showing the Limb Buds, Lateral Ridges, and Primitive Segments.

grow into each limb bud from the muscle-plate and skin-plate (dermatome) of the segments which are situated opposite the origin of the bud. Each corresponding segment of the spinal cord also sends to the limb bud a nerve process. At least seven body segments contribute to the formation of each limb (Fig. 439). Outgrowths from the myotomes into the limbs have been observed only in the embryos of lower vertebrates; their occurrence in higher vertebrates is inferred. When the arm musculature becomes apparent as a mass in the 6th week, it shows no signs of separate segmental origin.

Changes in External Conformation.—In the 5th week (Fig. 448) the limb buds are unsegmented; in the 6th a constriction marks the hand off; the position of the elbow being indicated in the same week. In the 7th week the fingers appear as thickenings in the *webbed* hand, the middle digit being indicated first. They become free at the end of the 8th

also Bardeen and Lewis, 1901, vol. 1, p. 1; *Keibel and Mall's Manual of Embryology*, vol. 1, 1910.

week; occasionally they remain attached, the child being born with its fingers in a **syndactylous** condition. The shoulder remains buried in the body wall; the skeletal structures of the arm and thigh are the first to be differentiated; those of the forearm and leg precede the cartilaginous differentiation of the shoulder and pelvic girdle. In all the embryological changes the upper extremity is nearly a week ahead of the lower.

The Internal Differentiation of Tissues begins at the basal part of the limb and spreads towards the digits, the terminal phalanges being the

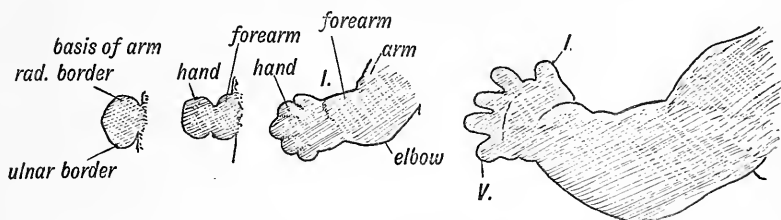


FIG. 448.—Four stages in the development of the Upper Limb—at the 5th, 6th, 7th and 8th weeks. (After His.)

last of the skeletal parts to become differentiated (8th week). The mesoderm or mesenchyme becomes condensed in the axis of the bud and forms the cellular basis, or **blastema**, of the limb bones early in the 6th week. The skeletal basis is continuous, but where joints are to be formed there occur opener formations in the arrangement of the cells. Centres of chondrification appear in the skeletal blastema of the arm late in the 6th week (shaft of humerus) and the leg in the 7th week (shaft of femur).

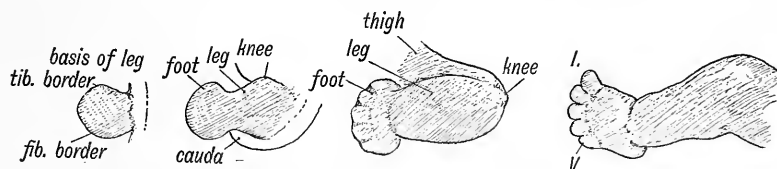


FIG. 449.—Four stages in the development of the Lower Limb—at the 5th, 6th, 7th and 8th weeks. (After His.)

The condition of the skeletal blastema of the arm of a human foetus in the 7th week of development is shown in Fig. 450. The centres of chondrification have appeared for the humerus, radius, ulna and certain of the carpal bones; the centres for the phalanges have not yet begun. The scapula, acromion and clavicle (outer part) are continuous; a common centre appears for scapula and acromion, the outer claviclar blastema is chondrified separately. Before the end of the 2nd month the cartilaginous bases of all the arm bones have appeared. Centres of ossification begin to appear in the latter part of the 2nd month, and correspond generally to the centres of chondrification. During the 3rd month the skeletal blastema between the chondrified bases of the bones, by a process of vacuolation within and between the cells, opens out into a cavity and forms the synovial

membranes of the joints (Fig. 473). By the end of the 6th week the proximal muscles, vessels and nerves

are appearing; a week later, they are also apparent in the distal parts of the limbs. The tissue left over, not included in these structures, forms their sheaths, and the fasciae and connective tissue of the limb. The processes of the nerve cells to form the nerve-fibres, and of the muscle plates to form the muscle-fibres, grow in very early (see Fig. 454). The blood vessels appear first as a capillary plexus surrounding the ingrowing nerve buds; in some mammals (the lemur, etc.) this embryonic plexus persists and forms the **plexus mirabile**. The limb vessels spread outwards from the segmental vessels.

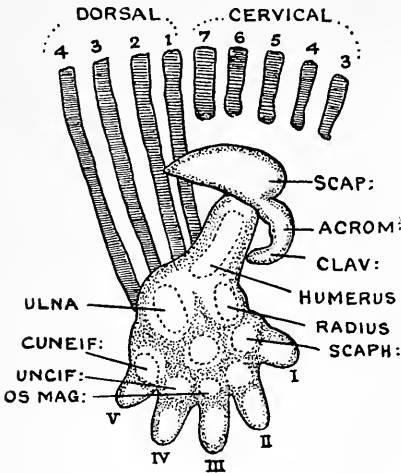


FIG. 450.—The Skeletal Blastema of the Upper Extremity of a Human Embryo in the 7th week of development. The centres of chondrification are indicated. (W. H. Lewis.)

Skeletal Blastema of Lower Extremity.—About the end of the 7th week the blastema of the ilium becomes joined to the costal masses of the 1st, 2nd and 3rd sacral vertebrae (Fig. 451). The scapula, which at the beginning of the 2nd month lies opposite the 4th, 5th, 6th, 7th cervical vertebrae, retains its freedom (Fig. 450). By the end of the 7th week the

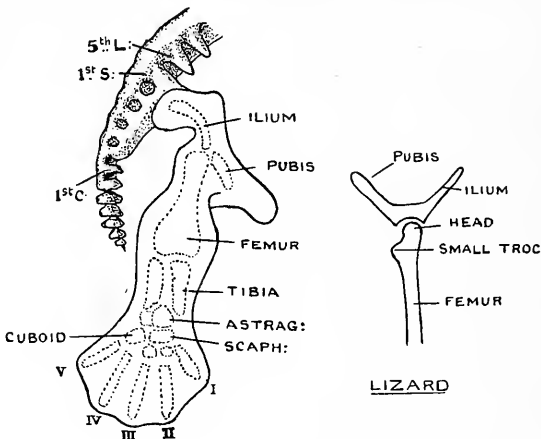


FIG. 451.—The Skeletal Blastema of the Lower Extremity of a Human Embryo in the 7th week—14 mm. long. (Bardeen.) Inset is the outline of the upper part of the lower extremity of a lizard. (Parsons.)

cartilage centres have appeared for the majority of the bones of the lower extremity (Fig. 451). The centres for some of the tarsal and for the phalanges are formed before the end of the 2nd month, the terminal

phalanges being the last. The acetabulum develops at the site of union of the iliac, ischial and pubic cartilages at the end of the 2nd month. At that time the femur has no neck—a condition seen in reptiles (Fig. 451). The neck begins to form early in the 3rd month. In the 3rd month the symphysis pubis is formed.

Torsion and Rotation of the Limbs.—As the limbs are developed, the extensor surfaces of the knee and elbow are directed upwards. If the body of an adult were placed in the prone position, it would be necessary, in order to restore the limbs to their embryonic position, (1) to draw them out at right angles to the axis of the body, (2) to rotate the leg **outwards** so that the extensor surface of the knee is directed upwards, with the great toe in front and the little toe behind. (3) The arm, on the other hand,

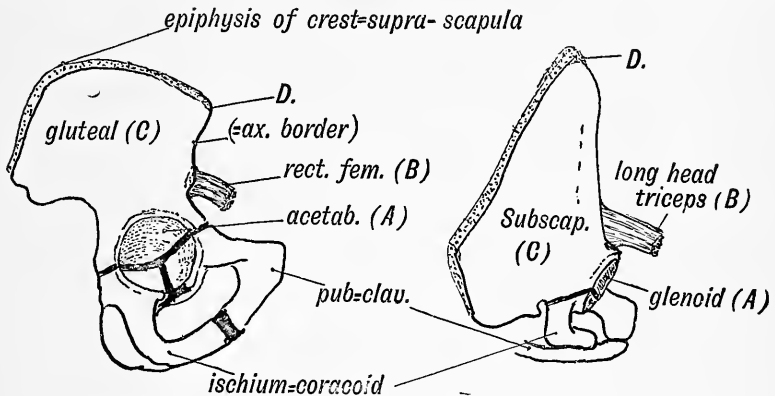


FIG. 452.—The Corresponding Points (A, B, C, and D) in the Ilium and Scapula.

would require to be rotated **inwards** to bring the elbow (extensor surface) into the dorsal position. The rotation which brings the embryonic limbs into the adult position appears to occur at the junction of the limb girdle with the trunk.

Rotation at the Limb Girdle.—To understand the extent of this rotation it is best to compare the scapula and ilium and pick out their corresponding points. The extensors of the thigh and arm may be taken as guides. The long head of the triceps and rectus femoris of the quadriceps manifestly correspond; their points of origin—the anterior border of the ilium and axillary border of the scapula—may be regarded as homologous points. The other corresponding points are shown in Fig. 452. The sacral articular surface of the ilium corresponds to part of the supra-spinous fossa. To restore the limb girdles to their primitive and corresponding positions, the scapula has to be rotated so that its axillary or posterior border comes to occupy the position of its spine, while the ilium has to be placed at right angles to the spine and its anterior border rotated outwards until it occupies a position corresponding to the axillary border of the scapula. The free edge of the spine represents a former border of the scapula; the supra-spinous blade of the scapula appears first in mammals.

There is a manifestly spiral twist in the humerus, but it is doubtful if this be in any way due to the torsion which the limb undergoes.

Professor Parsons¹ and Sir A. Geddes² have shown that although there is a direct correspondence in the elements of the upper and lower extremity, the correspondence is a reversed one—the right ilium representing a “mirror-image” of the right scapula which certainly is true. There is no evidence of a rotation of the elements of the limb-girdles during development. A reference to Fig. 453 will show that there is a correspondence between the structures on the distal border of the fore-limb and on the proximal border of the hind-limb. The subscapularis, teres major and latissimus dorsi (*A*), derivatives of a common flexor mass, correspond to

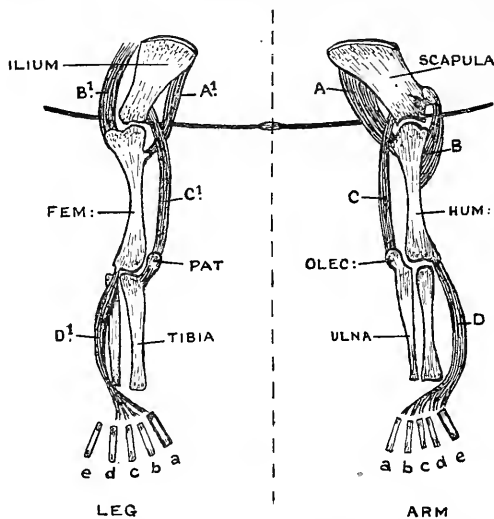


FIG. 453.—Diagram of the Fore and Hind Limbs of the same side to show the “Mirror-image” Relationship between their Constituent Parts. The vertical line passing through the umbilicus is regarded as the centre from which the two limbs have become differentiated. (After Parsons and Geddes.)

the ilio-psoas—also the derivative of a common flexor mass (*A*¹). The triceps and quadriceps (*C*, *C*¹) also agree; so do the olecranon and ulna with the patella and tibia. The specialization of the proximal digit of the hand to form a pollex, and of the first of the foot to form a hallux, occurs only in primates. The mirror-image theory particularly applies to the distribution of nerves. To explain this peculiar relationship, which exists between the fore and hind limbs of the same side in vertebrates, one is tempted to suppose that they represent anterior and posterior halves of a single primitive locomotory appendage; the line of separation is represented by the adjacent borders of the limbs. On such a theory the adjacent borders should be constituted alike.

Segmental Nature of the Limbs.—The nerves of the limbs, probably also the muscles, vessels and skin, are derived from a number of the

¹ F. G. Parsons, *Journ. Anat. and Physiol.* 1908, vol. 42, p. 388.

² Sir Auckland C. Geddes, *Journ. Anat. and Physiol.* 1912, vol. 46, p. 350.

primitive body segments. The 4th cervical to the 2nd dorsal contribute to the formation of the upper extremity ; the 1st lumbar to the 3rd sacral to the lower, but even in man the extent to which the most anterior and most posterior of each of these contributes to the limb varies considerably. Since the processes of the skin and muscle plates of these segments retain in the limbs (so we infer from the study of limbs of lower vertebrates) their original nerve supply, it is evident that the muscles and skin of the human limbs may be assigned to their original body segments by a study of the distribution of the nerves. Such a study has been carried out by a great number of men during the two last decades.¹ The primitive simple arrangement of muscle segments may be seen in the fins of certain

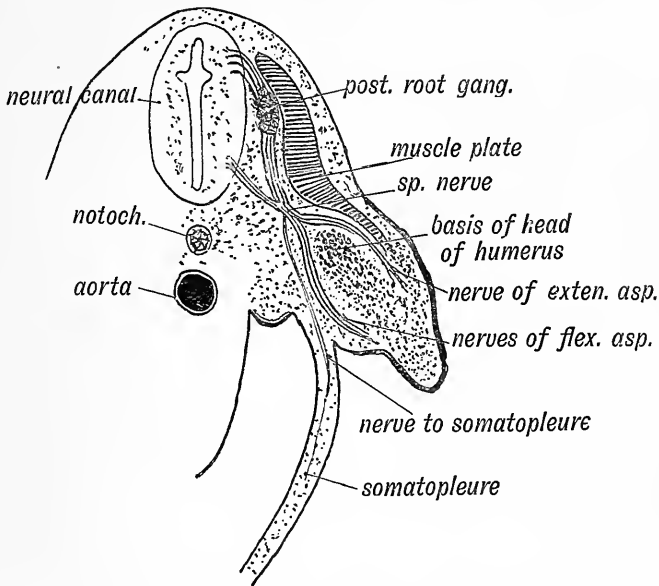


FIG. 454.—Section of the Arm Bud of a Human Embryo at the end of the 5th week. (Alex. Low.)

fishes, but in man these segments have been divided and combined and special muscles formed from them ; yet the primitive arrangement can be recognized.

Nerve Supply of the Limbs. The Arm.—It is important to note that the limb buds arise from the ventro-lateral aspect of the trunk (Fig. 454) near the junction of the somatopleure with the paraxial mesoderm. Therefore the nerves of the limbs are the nerves of the ventro-lateral zone—the lateral cutaneous branches of the typical segmental nerves (Fig. 455). The muscles are derived from the ventro-lateral sheet, which gives rise to all the muscles of the body wall. As soon as the limb buds appear, bundles of fibres from the anterior and posterior nerve roots of the corresponding

¹ For references see Geddes, *Journ. Anat. and Physiol.* 1912, vol. 46, p. 350 ; also the researches of Bolk, *Morph. Jahrb.* from 1894 to 1898 ; A. T. Kerr, *Amer. Journ. Anat.* 1918, vol. 23, p. 285.

body segments enter them and keep time with their growth. The limb nerves are at first so large in comparison with the size of the limb bud that they are crowded together and already form a plexus (Figs. 456, 457). As they enter the bud, the nerves encounter the condensed skeletal blastema at its base and divide into a dorsal or extensor set and a ventral or flexor set (Figs. 454, 455).

The relationship of the segmental nerves to the arm bud in the 6th week of development is shown in Fig. 456—a drawing taken from Professor Streeter's research.¹ The base of the arm is then situated in the cervical region; the hypoglossal nerve issues almost at its anterior border. The arm descends tailwards during the 2nd month, the nerves consequently

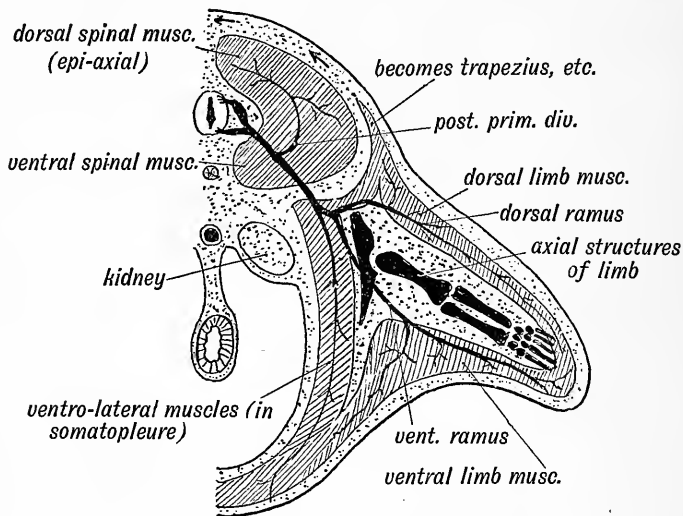


FIG. 455.—Schematic Section to show the primitive grouping of the Nerves and Musculature of Limbs. (After Kollmann.)

undergoing an elongation. The ventral divisions of the spinal nerves from the 5th cervical to the 1st dorsal have entered the bud, and already the chief nerves can be traced. The brachial plexus is formed; the interlacing of fibres does not arise owing to a compression of the nerves due to a lack of room, but represents a physiological or functional adaptation. Professor Goodrich² found that in fishes only the posterior root or sensory fibres entered into the plexiform arrangement—the motor or ventral fibres proceed into the limb without exchanging fibres. By the beginning of the 3rd month all the muscles and nerves are differentiated. In Fig. 455 the distinction between the nerves of the extensor and flexor aspects of the limb is shown.

In Fig. 457 the bud of the hind limb of the same embryo is represented. It will be seen that the stage of development is less advanced than in the arm. The crescentic base of the limb is in relationship with the spinal

¹ Geo. L. Streeter, *Amer. Journ. Anat.* 1908, vol. 8, p. 285.

² See reference on p. 425.

nerves from the 1st lumbar to the 3rd sacral. The crural and sciatic plexuses are continuous; their separation occurs in the 7th week, when the ilium becomes attached to the costal processes of the sacrum.

The nerve supply assists to indicate the body segments from which the arm is developed (Fig. 458). The 4th cervical is the most anterior, the 2nd dorsal, sometimes it is the 3rd, is the most posterior segment. Hence the arm is produced from seven, or more commonly eight, segments in all. Each segment contributes from its nerve, its muscle plate and probably also its artery (see p. 250). The typical distribution of a segmental nerve to the limb bud is shown diagrammatically in Fig. 455. Each segmental nerve, as is the case with the typical lateral cutaneous nerves, divides into a **dorsal** division for the extensor muscles, and **ventral** for the flexor muscles. The nerves to the extensor muscles form the dorsal divisions and cord of the brachial plexus; the nerves to the flexor muscles form the ventral divisions and the outer and inner cords. The processes to the limbs from

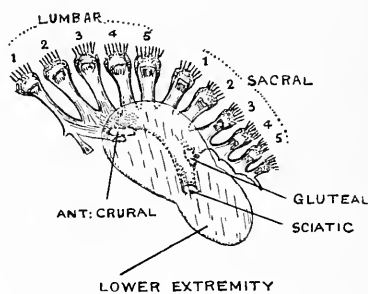
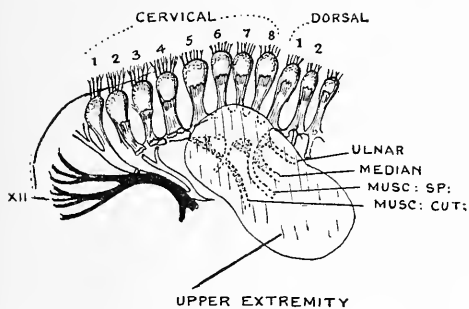


FIG. 456.—The Arm Bud and its Nerves in a Human Embryo in the 6th week of development. (After Streeter.)

FIG. 457.—The Bud of the Lower Extremity with its Relationship to Spinal Nerves in a Human Embryo in the 6th week of development. (After Streeter.)

the skin plates and muscle plates are also divided into dorsal and ventral sets; the one set making up the extensor aspect of the limb; the other, the flexor aspect.

Clinical and experimental research have shown that each of the seven or eight segments contributes to the cutaneous supply of the limb. The classical investigations of Sherrington¹ into the segmental distribution of the sensory nerves in the limbs of apes, showed that they are arranged in a definite and orderly manner (Fig. 459). The sensory distribution of the spinal nerves in the human arm is shown diagrammatically in Fig. 458. The distribution of the motor nerves of each segment is fully described in anatomical text-books.

Only three anomalous points in the arrangement of nerves in the upper limb require attention: (1) The segments which supply nerves for the arm are nearly constant. The extent, to which the 4th cervical and 3rd dorsal contribute, varies; the degree of variation is markedly less than in the lower limb. (2) A part of the musculo-cutaneous nerve frequently joins

¹ Sherrington, *Journ. of Physiol.* 1892, vol. 13, p. 621.

the median below the insertion of the coraco-brachialis; this communication is frequently seen in lower primates; its meaning is not known. (3) A communication between median and ulnar in the forearm is also common and is seen constantly in some primates. The communicating branch passes with the deep branch of the ulnar nerve to the palm. It is also manifest that there is a correspondence between the musculo-spiral nerve

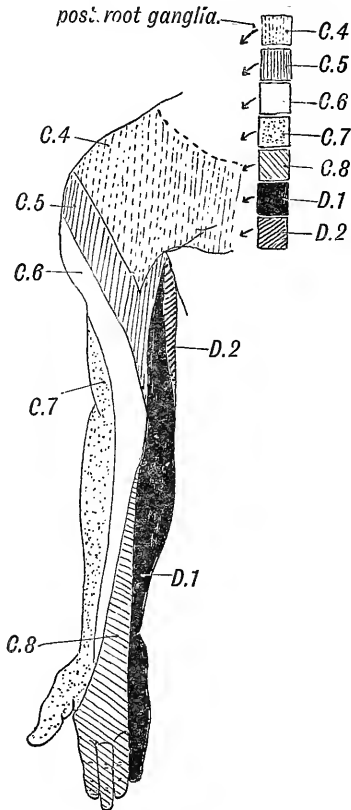


FIG. 458.—The Distribution of the Posterior Roots of the Spinal Nerves on the Flexor Aspect of the Arm.

on the proximal border of the arm and the sciatic on the distal border of the leg.

The Formation of Nerve Plexuses¹ depends on the following factors: (1) Each skin segment is supplied not only by its own nerve, but by the nerve of the segment in front of it and behind it. (2) A muscle segment, such as may be seen in the rectus abdominis, is supplied by its own and the two adjacent nerves, the fibres forming a plexus before entering the muscle. (3) Each muscle is formed by the combination of parts of two or more

¹ H. Braus, *Verhand. Anat. Gesellsch.* 1910, p. 14 (Origin of Nerve-Plexuses).

segments, and therefore its nerve rises from two or more spinal nerves. (4) The muscles of the limbs have migrated from their original positions and carried their nerves with them. (5) Most important of all, the afferent or sensory fibres from a muscle have to be linked to the centres of all the muscles which act as its antagonists or coadjutors. All these influences have led to the nerve fibres being assorted into definite cords at their first outgrowth.

Nerve Supply of the Lower Limb.—Usually ten segments contribute to the nerve supply of the lower limb—the 12th dorsal to the 4th sacral (Fig. 460). The sensory nerves are derived from these segments; the motor nerves begin at the 1st lumbar segment and end at the 3rd sacral. There is a considerable variation in the number of body segments or vertebrae to which the lower limb is attached; usually it is the 25th vertebra which becomes the 1st sacral, but it may be the 26th or 24th (p. 55). Of these

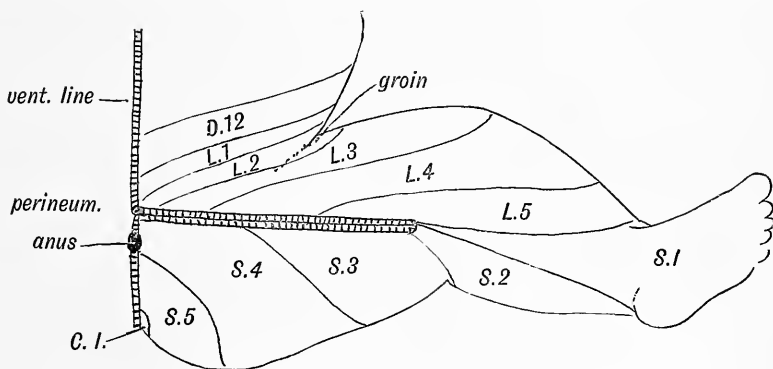


FIG. 459.—Diagram to show the typical manner in which the Posterior Nerve Roots are distributed in the Lower Limb (based on Sherrington's researches into the Sensory Distribution of the Limb Nerves of Apes).

three forms, the first is the normal type (25th); the second the post-fixed type (26th); the third the pre-fixed type (24th). There is even a greater variation in the segments which contribute nerves to the limb; the **normal** motor segments are the 1st lumbar to the 3rd sacral; in the **post-fixed type** (more common than the next) the motor segments commence at the 2nd lumbar and cease at the 4th sacral; in the **pre-fixed type** the motor segments commence at the 12th dorsal and end at the 2nd sacral. The spinal nerve which bifurcates and joins both lumbar and sacral plexuses is known as the **nervus furcalis**. In the normal type it is the 4th lumbar; in the pre-fixed type it is the 3rd lumbar; in the post-fixed type the 5th lumbar.

The **nervus bigeminus**, normally the 4th sacral, may also vary in a corresponding manner.

The nerves to the extensor surface of the lower limb, the anterior crural (femoral), external popliteal (common peroneal), etc., represent the **dorsal divisions** of lateral cutaneous nerves (Fig. 455). The nerves to the adductor and flexor aspects, the obturator and internal popliteal (tibial), represent

the **ventral divisions**. In a considerable number of individuals, the dorsal division (external popliteal) and ventral (internal popliteal) of the great sciatic separate in the pelvis, the external popliteal perforating the pyriformis.

The segmental distribution of the motor nerves in the lower extremities is given at length in text-books on anatomy. The muscular

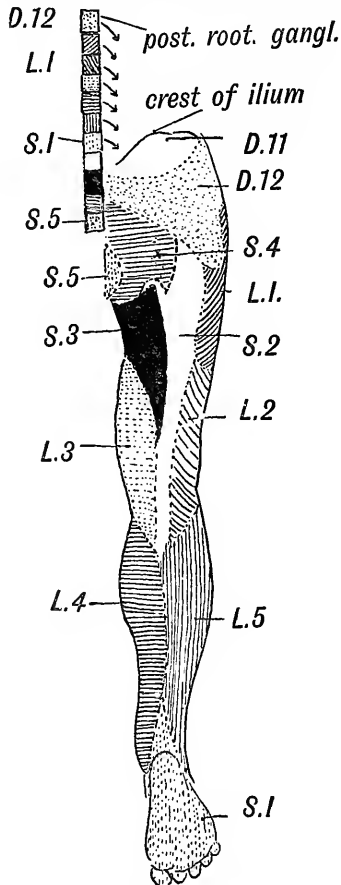


FIG. 460.—Flexor Aspect of the Lower Limb, showing the Sensory Distribution of the Segmental or Spinal Nerves.

segments correspond approximately in their distribution with those of the skin.

It will be remembered that the perineal region is developed behind the limb buds of the lower extremities (Fig. 439); hence its nerve supply from the most posterior nerve segments (3rd and 4th sacral).

Sherrington found that the posterior roots of the limb nerves were distributed in a regular and simple manner in apes. His results are applied

to the lower limb of a human foetus in Fig. 459. The actual distribution in man, which has been partially worked out by clinicians, varies considerably from what might be expected from Sherrington's results (compare Figs. 459 and 460).

In the human leg and foot there is a tendency for the nerve fibres destined for the outer digits to proceed in the external saphenous (sural) nerve instead of by the musculo-cutaneous (superficial peroneal). The **external saphenous** nerve may supply the 4th and 5th digits (the ancestral form) in a manner similar to the ulnar nerve in the hand; more frequently it is confined to the outer side of the 5th digit. The outgrowing fibres of the obturator nerve may be divided into ventral and dorsal parts by the blastema of the pubis. In such a case the more ventral fibres cross the ramus of the pubis and form the **accessory obturator** nerve.

Vessels of the Limbs.—When the limb buds are being formed in the 5th week they are permeated by a capillary network, which in the case of the arm is chiefly fed by the artery of the 7th cervical segment, while in the case of the leg bud the chief axial artery arises from a pelvic arterial plexus—soon connected with the internal iliac (hypogastric) artery. During the 6th week the main arteries of the limbs are being evolved from pathways in the primary capillary plexuses; by the end of the 8th week, all the important arterial channels have been laid down. Every student knows how frequently the arteries of the leg and arm depart from the arrangement which is regarded as normal. Comparative anatomy and embryology throw light on these arterial anomalies.¹

In Figs. 461, 462, the upper and lower limbs have been placed in corresponding positions—the extensor surfaces being directed upwards and a scheme of their arteries depicted in relationship to their skeletal elements. In each limb bud there is developed a main or axial artery, certain parts of which are suppressed in the 8th week while other accessory vessels are developed. The axial artery of the upper limb persists as the subclavian, axillary and brachial trunks, but in the lower limb the corresponding trunk (Fig. 362) is suppressed, as Professor Senior has shown, during the 8th week of development—save for the sciatic branch of the internal iliac artery and the anastomotic chain along the sciatic nerve which links together branches of the sciatic and popliteal arteries. In the flexor aspect of the elbow, as in the corresponding space—the popliteal—of the lower limb, the axial artery undergoes a degree of suppression. In the popliteal space, as we know from Professor Senior's investigations, the axial artery passes deep to the popliteus muscle; the part which lies deep to the muscle becomes reduced during the 8th week and a new vessel develops superficial to the muscle. The part of the popliteal artery proximal to the popliteus muscle is derived from the axial vessel; the part lying on the popliteus from the new trunk. In the anticubital space the corresponding axial vessel disappears, the terminal part of the brachial

¹ For development of arteries see Prof. H. D. Senior, *Journ. Anat.* 1919, vol. 53, p. 131; *Amer. Journ. Anat.* 1919, vol. 25, p. 55; Erik Müller, *Anat. Hefte*, 1903, vol. 22, p. 377. For comparative anatomy of vessels in limbs of primates see articles by Dr. Manners-Smith, *Journ. Anat. and Physiol.* 1910, 1911, 1912, vols. 44, 45, 46; E. Goeppert, *Ergebnisse der Anat.* 1904, vol. 14, p. 170.

artery with its divisional trunks—the ulnar and radial arteries—representing later channels.

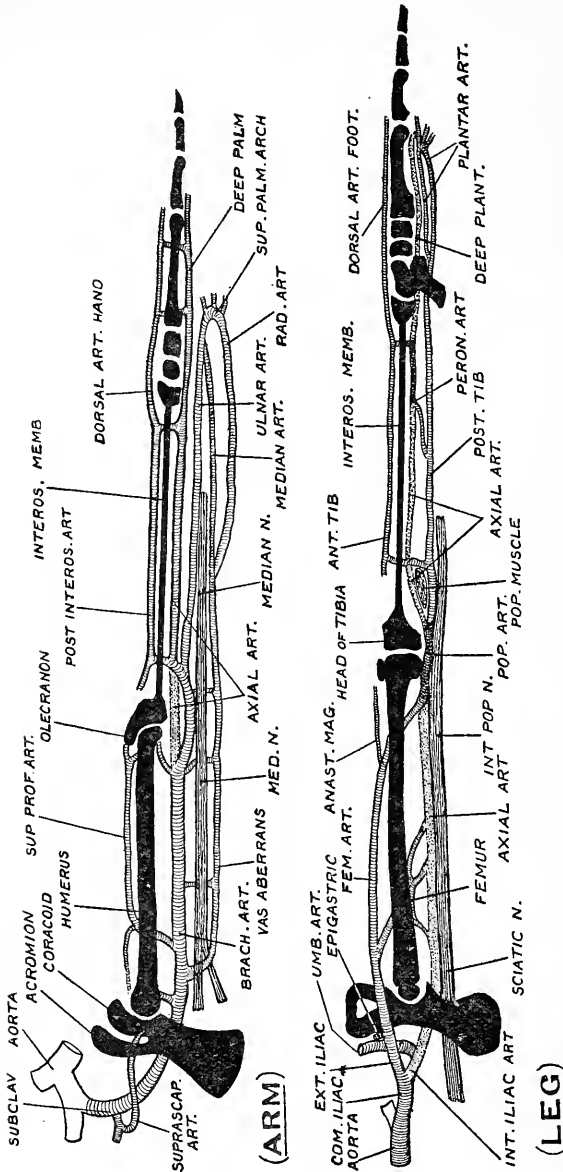


FIG. 461.—Scheme of Arteries of the Upper Extremity—the limb being so placed with its flexor surface downwards as to be comparable to Fig. 462.

FIG. 462.—Scheme of Arteries of the Lower Extremity. The parts of the axial vessel which are stippled become obliterated.

In the fore-arm the axial vessel is represented by the anterior (volar) interosseus, continued into the hand to give off the palmar interosseus

vessels—the primary blood supply of the hand. On the extensor or dorsal aspect of the interosseus membrane of the fore-arm develops the dorsal interosseus artery of the fore-arm fed by branches of the axial artery which perforate at the proximal and distal ends of the membrane (Fig. 461). In the leg the axial artery disappears, save its distal part, which is incorporated in the peroneal artery (Fig. 462). As in the fore-arm, perforating branches pass to the dorsal aspect of the interosseus membrane to form the anterior tibial artery.

Having thus traced the fate of the axial artery in each limb we now turn to the origin of the great secondary channels. The external iliac artery and its continuation, the femoral artery, open up a new channel to the lower limb along the course of the anterior crural or femoral nerve. The channel arises from the umbilical artery proximal to the origin of the internal iliac (the axial vessel) and by the end of the 7th week has effected a union with that part of the axial vessel which lies in the popliteal space (Fig. 462). In the upper limb there is no corresponding arterial trunk, although communications between the suprascapular (transverse scapular), circumflex and superior deep branch of the brachial artery may represent it. In both the leg and fore-arm more superficial secondary channels are formed—the ulnar and posterior tibial arteries and their branches which end in the superficial palmar and plantar arches (Figs. 461, 462). In all primates with the exception of man, the femoral artery, before piercing the adductor magnus, gives off a large branch—the **saphenous artery**—which accompanies the long saphenous nerve and turns to the extensor aspect of the leg above the internal malleolus where it becomes the dorsal artery of the foot. At no stage of human development does the saphenous artery serve as a main channel, but the superficial branch of the anastomotica magna, which represents this vessel in man, is more highly developed at the 8th week than it is at any subsequent period. The saphenous artery corresponds to the radial of the upper limb.

Vas Aberrans.—At a very early stage (7th week) there is developed along the superficial aspect of the median nerve an arterial anastomotic channel fed by a succession of branches which spring from the axial brachial vessel (Fig. 461). This channel frequently opens up in part, or even in its whole extent and gives rise to the greater number of arterial anomalies met with in the arm. The vas aberrans may replace the main artery, being known from the normal brachial artery by the fact that it lies superficial to the median nerve, whereas the usual vessel is deep to that nerve. The first ramus of the vas appears between the heads of the median nerve (Fig. 461). The ulnar or radial artery frequently arises from the brachial artery in the lower third of the arm; in such cases the upper part of the radial or ulnar vessels will be found to be formed out of the anastomotic channel. In the fore-arm the median artery may be of large size, ending in the superficial palmar arch; it, too, is formed out of the arterial anastomosis which is laid down in foetal life, superficial to the median nerve.

Superficial Veins.—During the 6th week the terminal margin of the limb buds is fringed with a venous plexus which becomes broken up by the

outgrowth and differentiation of the digits. The terminal plexus is drained by a vein which passes upwards on the fibular or peroneal margin of the limb, this marginal vessel becoming the superficial ulnar and basilic veins in the arm and the external saphenous vein in the leg. Later, radial and tibial marginal venous channels are formed, becoming the radial and cephalic veins in the upper limb and the long or internal saphenous in the lower. The cephalic vein originally crosses the clavicle and terminates in the external jugular vein as is the rule in apes, but later ends in the axillary vein, below the clavicle. In man only does the long saphenous vein terminate at the groin by piercing a hiatus in the fascia lata; in all other primates it ends above the internal (mesial) condyle of the femur by joining the femoral veins in Hunter's canal.

CHAPTER XXVII.

MORPHOLOGY OF THE LIMBS.

IN the previous chapter the chief events connected with the development of the limb buds in the human embryo have been noted and incidentally certain points relating to the morphology—primitive structure—of the limbs have been alluded to. In the present chapter we propose to deal with the more important problems relating to the pectoral and pelvic girdles, to the bones of the hand and foot, to the origin of joints and to the significance of certain muscular modifications.

Congenital Elevation of the Shoulder.¹—We have already seen that the arm of the human embryo is cervical in position—in this respect

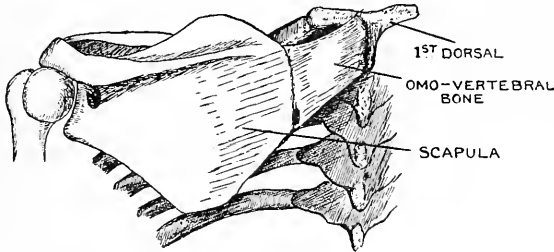


FIG. 463.—The Omo-vertebral Bone in a Case of Congenital Elevation of the Shoulder.

resembling the pectoral fins of fishes. It descends during the 2nd month, reaching its final position over the ribs in the 3rd month. Its descent is not only accompanied by an elongation of the brachial nerves, but also by a downward migration of certain muscles—originally placed in the neck—trapezius, serratus magnus, latissimus dorsi and pectoral muscles. The descent may be arrested. The condition, which is not rare in children, is often accompanied by irregularities in the formation of the cervical vertebrae—for the elongation of the cervical region to form a neck is related to the descent of the shoulder, of the heart, and of the diaphragm—and with the appearance of a skeletal element of the shoulder girdle which is present in certain fishes (dipnoi and selachians). This omo-vertebral element is represented in Fig. 463—from the classical case of

¹ The condition is often spoken of as *Sprengel's* shoulder. See H. A. T. Fairbank, *Brit. Med. Journ.* 1911, ii. p. 1533. For recent literature see D. M. Greig, *Edin. Med. Journ.* 1910, vol. 5, p. 236; 1911, vol. 6, p. 242.

Willet and Walsham (1880). In fishes this bone joins the supra-scapula to the occiput ; when it appears in man it is usually fixed to, or articulates with, the spinous processes of the lower cervical vertebrae. Man's upright posture has thrown the duty of constantly supporting the shoulder on the trapezius. Under certain circumstances it gives way, the shoulders then drooping. Symptoms may then arise from pressure of the nerves against the 1st rib—or a cervical rib.¹

Pelvic and Shoulder Girdles.—In the basal part of each limb bud a cartilaginous arch is developed. It consists of a **dorsal** and **ventral** part, the joint cavity for the articulation of the limb being situated at the junction of the two parts. Fishes retain this simple primitive form of girdle.

The **pelvic girdle** has undergone less modification from the primitive type than the shoulder girdle. The primitive type of pelvic girdle, such as is seen in the crocodile or lizard, and of which the mammalian type is a derivative, is shown diagrammatically in Fig. 464. For comparison the human girdle in the 7th week foetus is shown in Fig. 465.

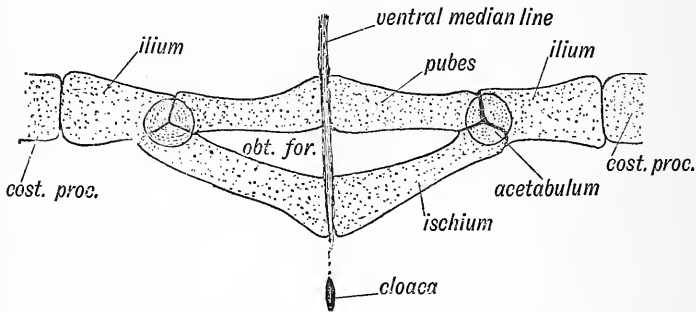


FIG. 464.—Diagram of the Pelvic Girdle of a Lizard.

The dorsal element consists of the **ilium** ; it is attached by ligaments to the costal process of one or more sacral vertebrae. In the ventral portion of the mesenchymal arch are developed two cartilaginous elements the **pubes** and **ischium**, both of which take part in the formation of the acetabulum (Fig. 464). Both reach the ventral median line in which a median bar of cartilage is developed (see Fig. 442).

In man the following changes may be noted : (1) The costal processes of the sacral vertebrae ($2\frac{1}{2}$ usually) have fused together to form the lateral sacral mass ; with these the ilium articulates (Fig. 451) ; (2) the vertebral border (crest) has become enormously elongated and gives attachment to abdominal muscles, cutting off the fibres of insertion of the external oblique which form the chief part of Poupart's ligament ; (3) the ischium does not reach the ventral line. In most birds, neither ischium nor pubis reaches the ventral line. The pubes fail to meet in cases of ectopia vesicae, just as the sternum is cleft in cases of ectopia cordis. The symphysis pubis is formed in the ventral line during the 3rd month. The cotyloid bone—os acetabuli—is formed in the Y-shaped cartilage between the three

¹ Prof. T. W. Todd, *Anat. Anz.* 1912, vol. 41, p. 385.

elements. It ossifies in the 13th year. Professor Howes has pointed out that it is this ossification which forms the pubic part of the acetabulum, and that it is really part of the pubes.

The **median pelvic bar**¹ corresponds to the sternum, and like it is of bilateral origin. In reptiles (Fig. 442) it is divided into anterior, middle and posterior parts. The anterior parts form the cartilaginous epiphysis of the pubic crest, which represent the marsupial bones, and correspond to the supra-sternal ossifications; the middle parts become the cartilaginous surfaces of the symphysis; the posterior parts (the hypoischium of reptiles) form the epiphyses on the pubic arch and ischial tuberosity (Parsons).

Congenital Dislocation of the Hip Joint.—Under this title two quite different groups of cases are included: (1) cases in which there has been

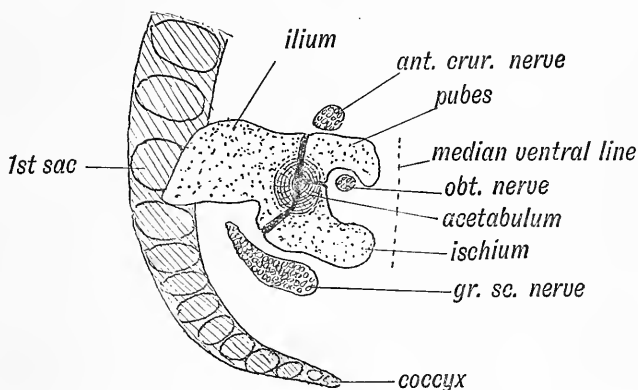


FIG. 465.—The Pelvic Girdle of a Human Foetus at the 7th week. (After Kollmann.)

an arrest of development of the parts entering into the formation of the hip joint; (2) cases which are produced during the act of birth. It is only the first group which is referred to here. In the 8th week—when the foetus is about 20 mm. in length, the three cartilaginous elements—ilium, ischium and pubis—meet in a Y-shaped acetabular suture, the pubic element being later in chondrifying than the other two. In the 9th week the hip joint is formed by (1) the appearance of a synovial cavity, (2) cartilaginous outgrowths from all three elements, but especially from the iliac—to form the acetabular cup; (3) the separation of the head from the shaft of the femur by the formation of the neck (see p. 429). The joint is completely formed early in the 3rd month. The synovial lining of the joint arises from an ingrowth of peripheral cells into the blastemal tissue between the acetabulum and head of the femur (Jenkins²). The outgrowth of the acetabular brim may be arrested at the reptilian stage reached in the 2nd month; congenital dislocation of the femoral head, which is fully formed, results. In the cases of cleft palate and imperforate

¹ Prof. T. W. Todd, *Amer. Journ. Physic. Anthropol.* 1920, vol. 3, p. 285 (age changes in pubic bone).

² G. T. Jenkins, *Brit. Med. Journ.* 1906, vol. 2, p. 1702.

anus (and this is a similar case) human development is arrested at a reptilian stage. The condition has an obscure relation to the development of the female sexual characters; 90 % of cases occur in female infants.

Shoulder Girdle.—The duckbill (ornithorhynchus) shows the most generalized type of mammalian shoulder girdle; it resembles closely the primitive reptilian type; from such a form the various types of mammalian shoulder girdle were probably evolved.

The dorsal part of the arch consists of (1) **scapula**, (2) **supra-scapula** (Fig. 466). The supra-scapula is represented in man by the cartilage along the vertebral border; it ossifies in the early years of manhood. The supra-spinous part of the scapula appears first in higher mammals; it is produced late in the development of the scapula (in the 3rd month of foetal life) by the upgrowth of the supra-spinous blade of the scapula; it is not represented in the pelvic girdle. The dorsal segment of the

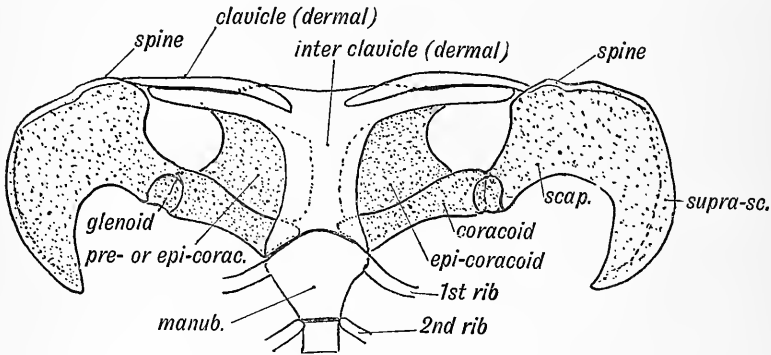


FIG. 466.—The Shoulder Girdle of Ornithorhynchus.

pelvic girdle becomes fixed to the costal processes; the corresponding part of the scapula remains free.

In the typical reptilian shoulder girdle, as in the pelvic (Fig. 464), two elements are formed in the ventral part of the arch—a posterior part—the **coracoid**, corresponding to the ischium, and an anterior—the **pre-coracoid**, corresponding to the pubes.¹ Both elements reach the ventral median line in which the sternum is developed (p. 419). In ornithorhynchus the coracoid element is represented by two bones—the coracoid and epicoracoid—the second of which is formed from the anterior end of the sternal bar and therefore corresponds to the suprasternal ossification of man.

¹ I have repeated the statement made in former editions, but the reader will perceive if the mirror-image correspondence is true (p. 430), that the ischium on the distal side of the pelvic girdle corresponds with the coracoid on the proximal side of the shoulder girdle—as stated above—but the representative of the pubis should be on the distal—not on the proximal side of the shoulder girdle as the clavicle is placed. I am convinced that there is no pubic representative in the shoulder. Developmental phenomena show that the clavicle is a new formation. Dr. D. M. S. Watson (reference p. 425) has shown that in the evolutionary history of the shoulder girdle the precoracoid is the first element to reach the mid ventral or sternal line and that later it is supplanted by the coracoid element. He regards the epicoracoid of ornithorhynchus as corresponding to the precoracoids of amphibia.

The dorsal extremity of the coracoid helps to form the glenoid cavity; its ventral articulates with the presternum. In man and all higher mammals, in which mobility of the fore limb is of advantage for speed and free movement, the coracoid element is much reduced. It forms merely a process on the scapula, which it joins in man about the 15th year. It still enters into the formation of the glenoid cavity, the articular part (supra-glenoid) having a separate centre of ossification which appears in the 12th year. It is possible that the costo-coracoid ligament may be derived from the ventral part of the coracoid element—the part which articulates with the sternum in the duckbill. The **precoracoid** in the shoulder girdle of a lizard corresponds to the pubic element in the pelvis. The precoracoid, which, like all the primitive elements of the pelvic and shoulder girdle, is formed in cartilage, has been partly or entirely replaced

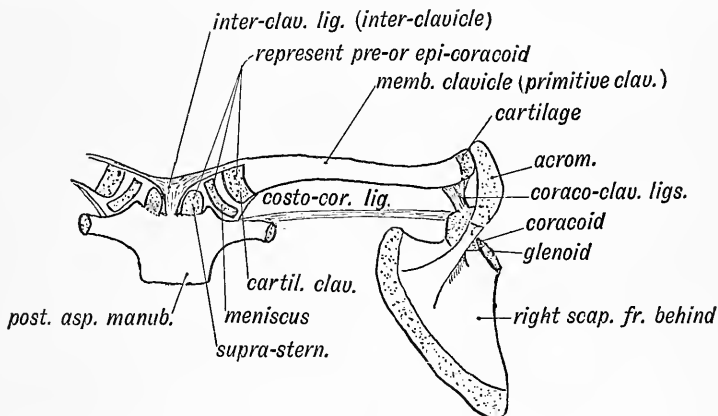


FIG. 467.—The Parts in the Shoulder Girdle of a Human Foetus which correspond with those of Ornithorhynchus.

in all mammals by the development over it of the clavicle, a dermal or membrane-formed bone, the first of all the bones to ossify. There is thus no true representative of the clavicle in the pelvis. The interclavicle so strongly developed in the ornithorhynchus and in the “merry-thought” of the fowl is also a dermal bone. It is represented in man by the interclavicular ligament.

In order to give greater mobility and speed to some four-footed mammals, the clavicle has been reduced to a ligamentous band, except at its extremities (rabbit, dog, etc.). In climbing animals, and those in which the power of grasping or embracing is highly developed, the clavicles are fully developed.

Clavicle.¹—At the beginning of the 7th week the clavicle is represented by a cellular or blastemal bar passing from the neighbourhood of the acromial process of the scapula to end ventrally in the anterior end of the sternal blastema. Professor Fawcett found that during the 7th week,

¹ For development of clavicle: Prof. E. Fawcett, *Journ. Anat.* 1913, vol. 47, p. 225; Dr. N. C. Rutherford, *ibid.* 1914, 48, p. 355; for sexual characters Prof. F. G. Parsons, *ibid.* 1917, vol. 51, p. 71.

when the embryo is 15 mm. long, two centres of chondrification appear in the clavicular blastema, quite close to each other, one corresponding to the termination of fibres of the sternomastoid, the other to the ending of fibres of the trapezius. Before proper cartilage has had time to form centres of ossification appear in the adjacent margins of the two precartilaginous masses, the two ossific centres uniting in a few days. From this double centre ossification spreads during the 8th week towards the sternum and towards the acromion, ossification being preceded by a true formation of cartilage.

There is a malformation of the clavicle which throws light on its double nature. In the remarkable disorder of growth known by the cumbersome name of **cleido-cranial dysostosis**¹ the clavicle is made up of two parts—an outer and inner, united by a fibrous band which may form only a short ligament, or may even represent the middle two-thirds of the bone. In such cases all the bones of the skeleton which are formed in membrane—

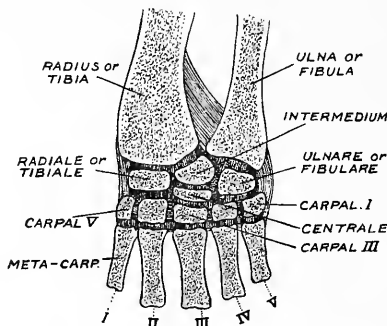


FIG. 468.—The Carpal Bones of a Tortoise.

especially those of the cranial vault—are imperfectly ossified. The condition in this disease suggests that the clavicle is a compound bone made up of outer and inner elements, and that arrest has occurred before the two elements have become joined. In cleido-cranial dysostosis some condition occurs which arrests the union of the two ossific centres; as ossification in cartilage proceeds normally in such cases we may presume that in spite of the appearance of cartilage in the clavicle, it was originally a membrane bone.

The **acromion process** is ossified from several centres which appear in the years of adolescence; the epiphysis so formed may be united to the spine by fibrous tissue only. This occurs in over 8% of subjects (Symington), and may be mistaken for a fracture of the process. The coracoclavicular ligaments may be derived from the precoracoid element.

Hand and Foot.—The hand and foot of man, as is the case in all primates, retain the primitive arrangement of elements much more closely than do most other mammalian orders. The primitive type of hand or foot, out of which the various forms found in mammals have been modified, are seen in such reptiles as the lizard or tortoise (Fig. 468). In the hand

¹ D. Fitzwilliams, *Lancet*, 1910, vol. 2, p. 1466.

of man the same bones are to be seen as in the tortoise, and in the same order of arrangement, with some exceptions. The elements in the foot of a typical lizard resemble closely the arrangement seen in its hand; the same elements are present even in the highly modified human foot. The hand and foot bones have undergone great specialization in most mammals. In the evolution of the horse, for instance, one lateral digit after another has become vestigial, leaving the central digit enormously enlarged and specialized to form the lower part of the extremities. In ruminants the 3rd and 4th digits have become predominant; the rest of the digits have become reduced until only traces of them are left; in rodents the hallux is vestigial. The hallux and pollex are the mammalian digits most liable to undergo retrogression. In man, on the other hand, the hallux and pollex find their greatest development.

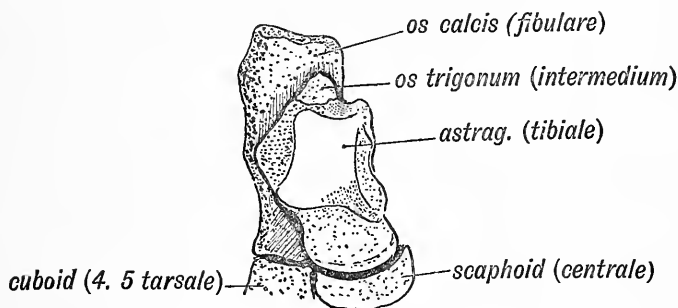


FIG. 469.—The Os Trigonum and other Bones of the Tarsus.

Comparison of the Tarsus and Carpus.¹—Both are the derivatives of such a typical form as is shown in Fig. 468. In the typical tarsus or carpus there occur the following bones :

1. **Radiale or Tibiale** forms the scaphoid in the hand and astragalus in the foot.

2. **Intermedium** forms the semilunar in the hand; in the foot it is much reduced and usually unites with the astragalus to form the external tubercle of that bone. It may remain separate and form the **os trigonum** (Fig. 469).

3. **Ulnare** becomes the cuneiform in the hand, the os calcis in the foot. During the cellular and early cartilaginous stages in the development of the human tarsus, the os calcis is in contact with the fibula. In the hand the ulnare and intermedium are bound by fibrous bands to the ulna (Fig. 468); these bands assist to form the triangular fibro-cartilage; in the ankle the corresponding bands form the middle and posterior fasciuli of the external lateral ligament.

4. **Carpale or Tarsale I.** becomes the trapezium in the hand, the internal cuneiform in the foot. In the prehensile foot of apes, the hallucial articular surface is directed inwards for the movable big toe. This is also the case

¹ See note on p. 444 and Fig. 453. Papers on carpal and tarsal bones: see R. B. S. Sewell, *Journ. Anat. and Physiol.* 1906, vol. 40, p. 152 (Astragalus); T. Manners-Smith, *Journ. Anat. and Physiol.* 1907, vol. 41, p. 255 (Navicular of Foot); H. M. Johnston, *Journ. Anat. and Physiol.* 1907, vol. 41, p. 59 (Scaphoid of Hand).

during the foetal development of the human foot (Leboucq). At no period of development is the hallux of man directed inwards and separated from the other toes. In man the great toe resumes a primitive position, and its metatarsal lies in line with the metatarsal series.

5. **Carpale or Tarsale II.** forms the trapezoid in the hand, the middle cuneiform in the foot.

6. **Carpale or Tarsale III.** forms the os magnum in the hand, the external cuneiform in the foot.

7. **Carpale or Tarsale IV. and V.** have united in both hand and foot to form the unciform and cuboid. This union occurs in all mammals. The unciform process has a separate centre of chondrification (Lewis). In the cat and carnivores the scaphoid and semilunar unite together, a union which may occur in man. In the foot an intimate union persists at the junction of the os calcis, cuboid and scaphoid until late in the 3rd month; in the cartilage of union a separate tarsal element may develop.¹

The **Os Centrale** is situated between the first and second rows of the carpal or tarsal bones (Fig. 468). In the foot it forms the scaphoid—a bone which plays an important part in the formation of the plantar arch—but is yet remarkably late in beginning to ossify, viz. about the 3rd year. It appears at the end of the 6th week as a separate cartilage element of the human carpus, but at the end of the 2nd month it has joined the dorsal and distal aspect of the scaphoid of the hand. It may be occasionally detected as a tubercle on the dorsal aspect of the scaphoid, or even as a separate bone. It is a separate bone in the carpus of all primates except the gorilla, chimpanzee and man. There are two centralia in lower vertebrate forms. The styloid process at the base of the 3rd metacarpal bone may occur as a separate ossification (*os styloideum*).

The **Pisiform** (ulnare laterale of Forsyth Major) is of doubtful nature. It is possible that in a very early stage of the evolution of mammals there were more than five digits—one behind the little finger—post minimi digiti; and another on the radial side of the hand—a prehallux. Supernumerary digits, when they appear, are commonly situated on the radial side of the thumb or ulnar side of the little finger, but they may represent merely a fission of the normal pollex or little finger. The pisiform has been regarded as the vestige of a post-minimal digit; the sesamoid on the trapezium, in which a slip of the extensor ossis metacarpi pollicis ends, as a remnant of a prehallux. It is possible also to regard the pisiform as a sesamoid developed in the tendon of the flexor carpi ulnaris—for that muscle is originally a flexor of the metacarpus and ends on the 5th metacarpal—the pisimetacarpal ligament representing the terminal part of the tendon. The pisiform, however, is developed with the rest of the carpal bones and before the tendon of the flexor carpi ulnaris. In mammals generally, but not in man, the pisiform articulates with the ulna as well as the cuneiform, and its synovial facet opens into the wrist joint. It may be represented in the foot by the heel epiphysis of the os calcis. The gastrocnemius, which represents the flexor carpi ulnaris in the leg, is also

¹ For extra carpal and tarsal bones see Pfitzner, *Morphol. Arbeiten*, 1896, vol. 6, p. 245.

primitively a flexor of the metatarsus; the long plantar ligament, from which it is separated by the growth of the heel, represents the continuation of its tendon.

Eversion of the Foot and Development of the Arch.—The human foot has been highly modified for upright progression. The chief modifications are :

(1) Gradual **eversion** of the foot, so that the sole can be applied to the ground. Even at birth—and for some time after—and always up to and before the 7th month of foetal life, the soles of the feet are inverted, so that when the foetal limbs are in their natural position they are directed towards the belly of the child. In club foot the natural process of eversion does not take place. The ape's foot is kept normally in the inverted position,

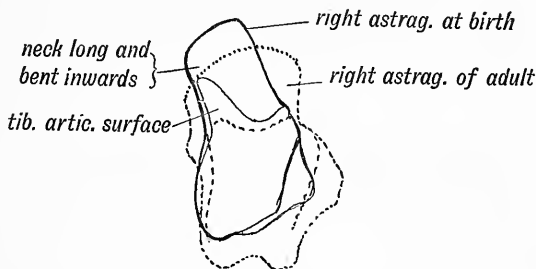


FIG. 470.—The Foetal and Adult (in dotted outline) Forms of the Astragalus contrasted.

an adaptation for prehension. The following factors assist in producing eversion :

- (a) The neck of the astragalus (Fig. 470), which in the foetal foot is long and directed downwards and inwards at an angle to the axis of its body, becomes relatively shorter and directed more in line with the axis of the articular surface of its body (Fig. 470). Further, the lateral border of the tibial articular surface of the astragalus is prominent in the foetus; the mesial border is much the lower; a growth upwards of the mesial border causes the astragalus and foot to rotate outwards (Lazarus).
 - (b) The bones on the inner side of the foot, particularly the scaphoid and internal cuneiform, grow more rapidly than those on the outer side of the foot—especially after birth. This tends to evert the foot and also to produce the longitudinal arch.
 - (c) A special evertor of the foot is produced—the peroneus tertius—a muscle peculiar to man. It is developed from the outer and lower fibular fibres of the extensor longus digitorum and represents part of the tendon of that muscle to the 5th toe. The peroneus brevis and longus may also assist, especially the latter, which in apes is a grasping muscle, acting as a flexor of the metatarsal bone of the hallux.
- (2) The tarsal bones of the human foot—especially the astragalus and os calcis—are of great size when compared with the tarsal bones of other

primates; while the digital or phalangeal elements, except in the case of the great toe, which is relatively of great size, have undergone retrogression. This is especially the case in the human little toe; some of its muscles are not infrequently fibrous, and the terminal phalanx may not be separated from the middle phalanx. The terminal phalanx is the last to be differentiated in development of the fingers and toes (in 3rd month).

(3) The plantar arches, both longitudinal and transverse, are produced. The arch of the foot is a human character. At birth the child is flat-footed when the weight of the body rests on its feet; the head of the astragalus touches the ground. When the muscles are removed by dissection the foot of the newly born child shows a well-developed arch (Russell Howard). The arch becomes stable as the child learns to walk. The chief factor in its production is the growth of the tarsal bones—especially of the scaphoid and internal cuneiform—and 1st metatarsal and the co-ordinated action of the muscles. Hence in rickets, where the normal tarsal growth is disturbed, the occurrence of flat foot. Amongst the structures which help to maintain the arch are :

- (a) The growth of the os calcis to form a prominent heel separates the tendon of the plantaris from its prolongation in the sole—the middle part of the plantar fascia, which assists in maintaining the arch. In lower primates the two parts are continuous, the tendon of the plantaris plying across the os calcis in a cartilage-lined groove.
- (b) The internal lateral ligament of the ankle (anterior part) and the inferior calcaneo-scaphoid ligaments undergo great development in man.
- (c) The flexor brevis digitorum which in lower primates arises principally from the long flexor tendons in the sole, has its origin completely transferred to the os calcis in man. It can thus act more powerfully in maintaining the arch. The flexor accessorius, a detached part of the flexor longus hallucis, is specially well developed and helps to maintain the arch of the foot.
- (d) The tibialis posticus, originally a flexor of the metatarsus, corresponding to the flexor carpi radialis in the hand, obtains a secondary attachment to the scaphoid. The tibialis anticus, which answers to the extensor ossis metacarpi pollicis, becomes permanently inserted into the internal cuneiform and metatarsal. Both of these muscles, thus modified, help to maintain the arch of the foot. So does the tarsal part of the tendon of the tibialis posticus.
- (e) The long plantar ligament, originally a part of the tendon of insertion of the gastrocnemius—also assists to maintain the arch.

(4) The development of the great toe and the peculiar arrangement of its muscles must also be regarded as adaptations in the foot to upright posture and progression.

CERTAIN FEATURES OF THE MUSCULATURE OF HUMAN LIMBS.

Muscles of the Pollex and Hallux.—The extensor ossis metacarpi pollicis corresponds to the tibialis anticus. The thumb muscle has commonly a carpal insertion as well as metacarpal. The extensor brevis or primi internodii pollicis is constant in man only; it is a segment of the extensor ossis metacarpi pollicis. The extensor brevis hallucis is not represented in the thumb.

Muscles of the Second Digit.—In the lower primates each finger has two extensors—a deep and superficial. The deep in the second digit becomes the extensor indicis; in the little finger it forms the extensor minimi digiti. The deep extensor muscles have disappeared in man from the 3rd and 4th digits, but occasionally reappear. In the leg the deep extensors have migrated to the foot, and form the extensor brevis digitorum. That for the little toe, however, has not descended; it is always vestigial, if present. It runs beneath or with the peroneus brevis, and is known as the peroneus quartus or **peroneus quinti digiti**. If the mirror-image theory is true it represents the extensor brevis pollicis.

Flexors and Extensors of the Metacarpus.¹—These have retained their primitive insertions in the hand; their modifications in the foot have been already mentioned. Both at the knee and elbow joint the origins of these muscles have undergone much shifting and migration.

Migration of Muscular Attachments.—Many of the human muscles acquire during development attachments to segments at a distance from those from which they are developed. The serratus magnus arises from 5th, 6th, 7th cervical segments; its attachment has extended backwards from the 1st rib until, in man, it reaches the 8th rib; the trapezius, originally situated in the neck, migrates backwards, and in the 7th week obtains an insertion to the shoulder-girdle, and before the end of the 3rd month its origin has reached as far backwards as the 12th dorsal spine along the median dorsal line. The latissimus dorsi migrates to the median dorsal line over the spinal musculature and reaches the spine and crest of the ilium. The diaphragm, which arises in the neck (4th and 5th segments) comes to be attached in the floor of the thorax. The facial musculature takes its origin in the hyoid arch. The subvertebral (hypaxial) musculature is a migrated part of the transversalis sheet. The omo-hyoid is attached at first to the sternum; it migrates along the clavicle and reaches (often it fails to reach) the upper border of the scapula. The migration of the subclavius has been in an opposite direction; originally it reached to the humerus. The case of the extensor brevis digitorum of the foot has just been mentioned. The flexor accessorius is a part of the flexor longus hallucis which has migrated to the sole of the foot. The opponens of the thumb and of the little finger is a separated part of the short flexor muscles of these digits. These are only a few of the more striking examples

¹ J. P. McMurrich, *Amer. Journ. Anat.* 1906, vol. 6, p. 407 (Plantar Musculature); J. P. McMurrich, *Amer. Journ. Anat.* 1904, vol. 4, p. 33 (Musculature of Thigh).

of the migration of the attachment of muscles, but the mechanism which brings about migration and the biotactic influence which is at work are unknown.

Vestigial and Abnormal Muscles of the Limbs and Trunk.—(1) The muscles of the human **ear and scalp** may be described as vestigial when compared to the development in other mammals. Although their action on the ear and scalp is feeble, yet they serve as most important bases into which certain psychological states are reflected.

(2) The **levator claviculae** (omo-trachelian) is a muscle which passes from the upper transverse cervical processes to the outer end of the clavicle or acromion process. It is well developed in climbing primates. It is

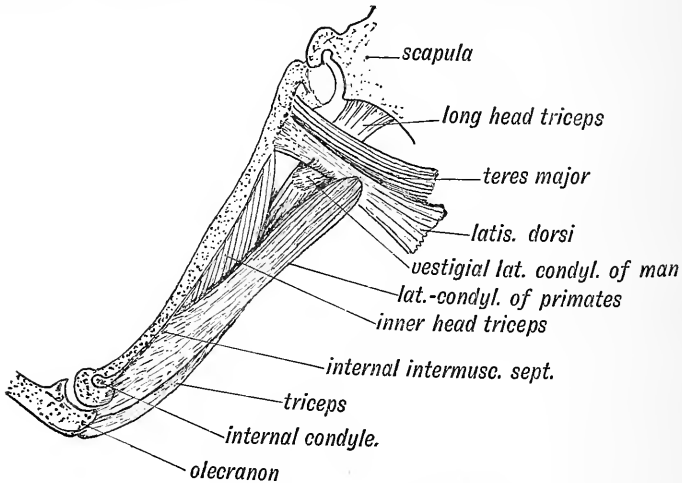


FIG. 471.—Latissimo-condyloideus Muscle.

not a common muscle in man. It can be recognized during life in the posterior triangle of the neck.

(3) The **latissimo-condyloideus** (dorsal epitrochlearis), a climbing muscle, is always represented in man, commonly by a fibrous bundle between the tendon of the latissimus dorsi and the long head of the triceps (Fig. 471). The bundle may be occasionally muscular. In apes it passes from the latissimus dorsi at the axilla to the inner aspect of the elbow and arm, which it retracts in climbing. It belongs to the same sheet as the coraco-brachialis. The **ligament of Struthers**—a strip of fibrous tissue over the internal intermuscular septum, above the internal condyle—represents part of the tendon of this muscle. The muscular slips occasionally found crossing the brachial or axillary artery from the latissimus dorsi to the coraco-brachialis or biceps are derivatives. Other slips found crossing the floor of the axilla, between the adjacent borders of the pectoralis major and latissimus dorsi, are parts of the muscular sheet out of which these two muscles are developed.

(4) The **pectoralis externus** arises from the 4-5-6 ribs and costal cartilages, beneath the axillary border of the pectoralis major. This is its normal

condition in most mammals, but in man it is commonly fused with, and forms part of, the pectoralis major.

(5) The **sternalis** is a remnant of the primitive rectus sheet (Fig. 445). The pectoralis major is formed from the same ventral longitudinal sheet as the rectus abdominis and sterno-mastoid. The fibres of the sternalis, which lie along the sides of the sternum, superficial to the origin of the pectoralis major, represent a persistent part of the primitive longitudinal sheet.

(6) In the **sterno-mastoid** four elements are recognized: sterno-mastoid, sterno-occipital, cleido-mastoid, cleido-occipital. The cleido-occipital fibres, which form part of the same sheet as the trapezius, are often absent. On the other hand, the cleido-occipital fibres may be continuous with the trapezius. The sterno-mastoid and trapezius muscles are developed in the occipital segments and are originally connected with gill arches.

(7) The **pectoralis minor** is sometimes inserted to the capsule of the shoulder and great tuberosity of the humerus as is the case in primates generally. The coracoid insertion, which is the usual one in man and also in the gorilla, is usually regarded as a secondary attachment, but Miss K. Lander¹ has shown that it is also found in primitive types of mammals. When the pectoralis minor is inserted to the coracoid, the former fibres of insertion become fused with, and form part of, the coraco-humeral ligament, which, however, is a distinct structure, and represents a specialized part of the capsule of the shoulder joint.

(8) In some apes (such as the Gibbons) the **biceps** has four heads—the two usual, the long and short, and two others, one from the inner border of the humerus and one from the bicipital groove. These two extra heads appear frequently in man.

(9) The **epitrochleo-anconeus** is frequently present. It crosses the ulnar nerve from the internal condyle to the olecranon.

(10) The **palmaris longus** and its homologue in the leg, the **plantaris**, are vestigial, aberrant in form, and often absent. The plantar and palmar fasciae represent their divorced tendons. The plantaris and palmaris undergo retrograde changes in the primates with the transformation of claws to nails.

(11) Each digit (fingers and toes) in lower primates, such as monkeys, is provided with three short muscles which arise from the carpus or tarsus. The three muscles are (Fig. 472): (1) a short flexor on the radial side of the digit; (2) a short flexor on the ulnar side; (3) a **contrahens** or adductor muscle (always absent in the middle digit). The ten short flexor muscles form a deeper sheet than the four contrahentes. Of this form the arrangement of the short muscles in the human hand is a derivative. The remnants in the human hand and foot of the contrahentes are: (1) The adductors of the 1st digit (pollex or hallux); (2) fibrous remnants of the others occur over the deep plantar or carpal arch (Fig. 472). The short flexors in man have become (1) the seven interossei; (2) the flexores breves (ulnar and radial) and opponens of the first digit; the flexor brevis and opponens of the fifth digit (see Fig. 472). The ulnar flexors of the thumb and great toe are absent or fibrous.

¹ *Journ. Anat.* 1918, vol. 52, p. 292.

(12) The **pyramidalis** is often absent in man or vestigial. It is the tensor of the linea alba.

(13) Remnants of the **extensors and flexors of the tail** may occur between the sacrum and the coccyx (p. 410).

(14) The **coccygeus** is vestigial; its superficial part forms the small sacro-sciatic ligament.

(15) Fibres of the biceps of the thigh may be followed into the **great sacro-sciatic ligament**. This ligament, which is almost peculiar to man—in other primates it is quite thin and slender—may contain fibres derived from the caudo-femoral group of muscles, such as the tenuissimus, a long strap-like muscle which passes from the coccyx to the femur and leg in lower mammals. The sacro-sciatic ligament is mainly derived from the great median sheet, out of which the middle layer of the lumbar fascia is also formed. Parsons regards the **short head of the biceps** as a derivative

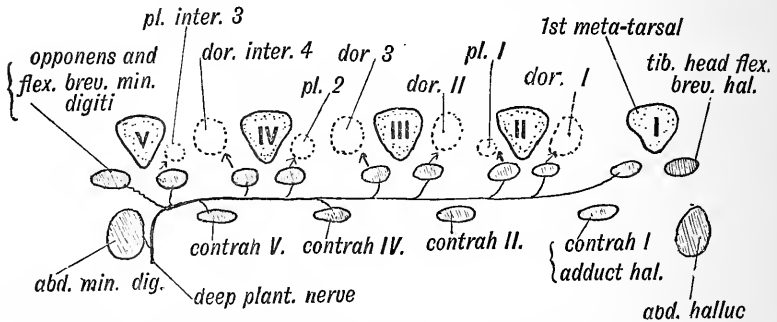


FIG. 472.—The Morphology of the Short Muscles of the Digits. The muscles shaded are those of the ape's hand or foot; the positions of the corresponding muscles in the human hand or foot are indicated by dotted outlines.

of the tenuissimus, while others regard it as part of the muscular sheet which forms the peroneal muscles. Amongst primates, the short head is found only in man, the anthropoids, and some South American apes. It corresponds to the brachialis anticus in the arm, and is supplied by the external popliteal nerve.

(16) The **psaos parvus** is also vestigial. It acts primarily as a flexor of the pelvis on the spine. It begins to disappear in those primates which assume the erect posture.

(17) The **scansorius** is a separated segment of the gluteus medius and minimus. It rises from the anterior border of the ilium and passes to the great trochanter. It corresponds to the teres minor. It is not constant in any animal.

(18) The **flexor brevis digitorum** to the little toe and the adductor transversus of the great toe are often fibrous.

The **Supra-condylar Process**¹ is well developed in lemurs, the lowest primates, and in mammals of many orders. Its function is unknown. It occasionally appears in man. Dr. Rutherford found it represented in a human foetus in the 9th week of development. It is developed from the

¹ T. Dwight, *Amer. Journ. Anat.* 1904, vol. 3, p. 221.

humerus about two inches above the internal condyle as a hook-like process of bone. It lies in front of the internal intermuscular septum, and when well developed the brachial artery and median nerve may pass beneath it, as they do in such animals as the squirrel and cat.

Development of Joints.—Each limb bone is formed from a centre of chondrification which appears in the 2nd month within the unjointed skeletal blastema of the limb bud. At these centres the mesodermal cells assume the characters of cartilage cells; growth proceeds most rapidly at the periphery of the cartilage centres; as the growing centres approach each other, part of the original blastema is left between them. This tissue, which may be named the **interchondral disc**, forms the first basis of a joint (Fig. 473). The cells in the peripheral part of the blastema condense and form a **perichondrium**—a membrane which surrounds growing cartilages. In the 8th and 9th weeks, joints begin to appear in the inter-

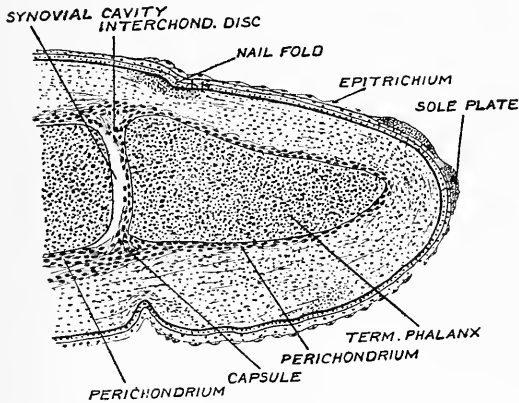


FIG. 473.—Sagittal section of Terminal Joint of Finger of Foetus in 10th week of development. (After Nicolas.)

chondral discs, the more important before the less important. The manner of formation is the same for all joints; in the periphery of the interchondral disc, the mesenchymal cells begin to disappear, giving rise to the synovial space which spreads towards the centre of the developing joint—the central part being the last to form. The perichondrium is continued from segment to segment over the interchondral discs and thus becomes the basis of the capsular ligament. At first the ends of the cartilages projecting into joint cavities are also covered by an extension of the perichondrium. Peripheral cells of the interchondral disc line the capsule and form the **synovial membrane**, the cells of which, even in the adult, show by their structure that they are cartilaginous in nature. In certain pathological conditions, the synovial villi give rise to cartilaginous nodules.

Interarticular Fibro-cartilages.—In every developing joint fringes of synovial membrane, representing remnants of the interchondral disc (intermediate plate), project in the gap between the articular margins of bones (Fig. 473). In the elbow joint they are present, even in the adult;

in the hip and shoulder joint they form the cotyloid and glenoid ligaments. In the knee joint they are much better marked, forming the semilunar cartilages. At the wrist joint the interchondral disc forms the **triangular fibro-cartilage**, but here it is possible that certain other elements are included. A nodule of cartilage, which may ossify, is present; within it certain ligaments which united the radius and ulna, and these two bones with the semilunar and cuneiform, have been included (Parsons and Corner). This cartilage is complete in man only; it plays a part in the mechanism of pronation and supination. In the **sterno-clavicular joint** two synovial cavities are formed, one on either side of the interchondral disc. In this case it is only in the higher primates that a complete interarticular disc is present. Two synovial cavities are also formed in the **temporo-mandibular joint**, the meniscus separating two joints, which are functionally

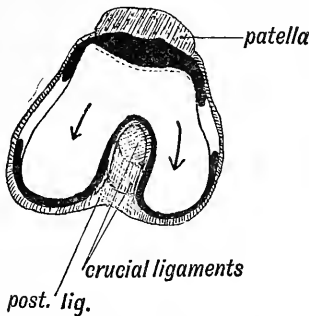


FIG. 474.—Showing the Origin of the Crucial Ligaments of the Knee.

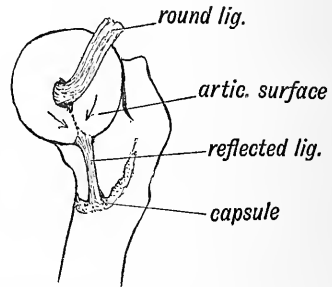


FIG. 475.—Showing the Origin of the Ligamentum Teres and Reflected Bundle of the Capsular Ligament.

different. The upper is for gliding movements, the lower for hinge-like movements.

Capsular Ligaments.—Certain parts of the capsule of every joint become thickened and specialized according to the strains to which the joint is subjected. Parsons found that it is the middle gleno-humeral ligament of the shoulder joint which becomes enlarged and projects within the joint of pronograde mammals. In man, the coraco-humeral ligament is by far the strongest. The anterior part of the capsule of the hip joint in man has to withstand the strain of the body when the thigh is extended in the upright posture. Part of it becomes specialized to form the ilio-femoral or Y-shaped ligament. In the knee joint the posterior part of the capsule is strengthened to prevent over-extension. The development of the condyles of the femur towards the popliteal space isolates a posterior part of the capsule which thus comes to lie within the joint and form the crucial ligaments (Fig. 474). The ligamentum teres, the best example of an **intra-articular ligament**, appears in the human foetus, as part of the capsule of the joint; in reptiles this foetal form is retained. The round ligament is isolated by the development of the head of the femur, which expands as a wing on each side of the ligamentum teres, and by the fusion of the wings isolates it from the capsule (Fig. 475). The **reflected ligament**,

on the under surface of the neck of the femur, is the part of the capsule with which the ligamentum teres was continuous.¹

Knee Joint.—In Fig. 476 is given a diagrammatic representation of the posterior aspect of the knee joint as seen in a primitive mammalian type. Three interarticular discs are shown; an internal tibio-femoral, an external tibio-femoral and a fibulo-femoral. When the fibula became excluded from the knee joint, the fibulo-femoral disc, from which fibres of the popliteus took origin, was included in the tendon of that muscle (Carl Fürst). The **popliteus** originally passes from the fibula to the tibia like the pronator quadratus in the forearm. The upper fibres migrate to the capsule and to the fibulo-femoral disc, and through the disc and its ligaments gain an attachment to the femur. Thus, instead of rotating the tibia on the fibula, the popliteus muscle now rotates the tibia on the femur. Occasionally the cavity of the human knee joint communicates with the superior tibio-fibular joint through the synovial diverticulum beneath the tendon of the popliteus. The upper end of the fibula is being

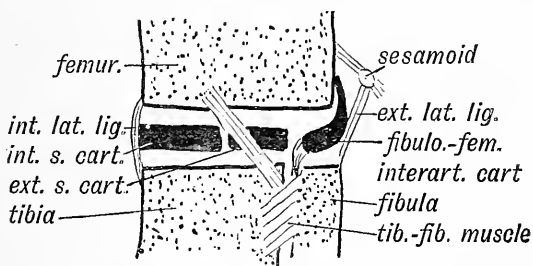


FIG. 476.—Scheme of a Primitive Mammalian Knee-joint to show (1) the Articulation of the Fibula with the Femur; (2) the Fibulo-femoral Interarticular Cartilage which becomes included in the Tendon of the Popliteus; (3) the Tibio-fibular Muscle out of which the Popliteus is evolved; (4) the division of the Tibio-femoral Interarticular Cartilage into external and internal Semilunar Cartilages. (Carl Fürst.)

excluded from the knee joint during the 8th week. There are five separate synovial cavities developed in this joint—one between the patella and femur, two between the femoral condyles and the primitive semilunar cartilages, and two between the cartilages and the upper extremity of the tibia. The five joints become continuous in the 4th month, the crucial and alar ligaments being derived from the primary septa between the cavities (Bardeen).² The external semilunar cartilage is circular in form and continuous with the posterior crucial ligament in primates, in which the power of rotation at the knee is highly developed; in man the circular form of the cartilage is lost and it only retains part of its continuity with the posterior crucial ligament (Parsons). The ligamentum mucosum, which in many mammals separates the knee joint into three compartments—two condylar and a patellar—is much reduced in man.

Ossification of Bones.—The simplest and most primitive manner in which bones pass from the cartilaginous to the osseous stage is seen in the

¹ See Walmsley, *Journ. Anat.* 1917, vol. 51, p. 61.

² See reference, p. 425.

carpus and tarsus (Fig. 477). Bone is entirely deposited within the cartilage by a process of **endochondral ossification**. The various stages in this process may be grouped as follows: (1) calcification of the intercellular matrix in the centre of the bone—a temporary phase in human ossification, but a permanent one in some fishes; (2) an invasion of vasoformative and osteoblastic cells which, commencing at a point beneath the perichondrium, reach the middle of the central area of calcification and form a centre of ossification (Fig. 477). The osteoblasts and their accompanying vessels, when the cartilage cells are absorbed, deposit bone in the spaces of the calcified matrix. A section through an ossifying and growing carpal bone shows (1) a centre of ossification; (2) a surrounding narrow area of calcification; (3) a peripheral area of actively growing cartilage; (4) a covering membrane or perichondrium. The processes of growth and ossification cease when the cartilage beneath the peri-

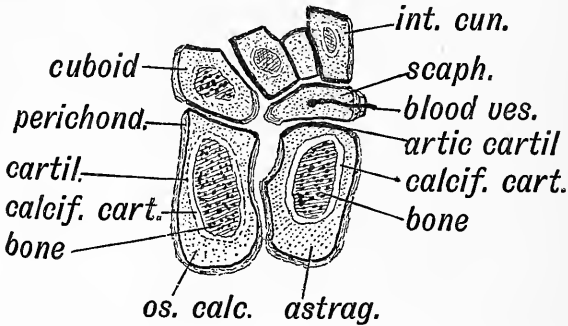


FIG. 477.—Section of the Tarsus at the 3rd year of development to show pure Endochondral Formation of Bone.

chondrium is completely transformed to bone. Not only are the tarsal and carpal bones formed thus, but so are the epiphyseal ends of all long bones.

In the shafts of long bones, to the process of endochondral ossification, another—the **ectochondral**—is added (Fig. 478, *A, B, C, D*). An endochondral centre is formed as in the tarsal bones, and from this centre the process extends rapidly in every direction. Some of the osteoblasts, instead of invading the cartilage, form a layer beneath the perichondrium, which surrounds the cartilaginous substance of the bone. The perichondrium now becomes periosteum; the deposit of periosteal bone leads to an increase in the thickness of the shaft (Fig. 478, *C*); the extension of the endochondral ossification into the growing cartilaginous ends of the bone leads to an increase in the length of the shaft. As the periosteal bone is deposited, the endochondral bone within the shaft is absorbed and a medullary cavity is formed, in which **red marrow** begins to appear in the 6th month (Fig. 478, *D*). The cartilaginous parts of the bone, at each extremity of the shaft, form the epiphyses. When the endochondral centres appear and grow within the epiphyses, a line of growing cartilage is gradually isolated between them and the endochondral centre of the shaft (Fig. 478, *D*). At the **epiphyseal line** the bone grows in length,

the addition being made solely at the shaft or diaphyseal side of the line. These growth discs should therefore be named, not *epiphyseal* but *diaphyseal* lines. By the formation of epiphyses at the ends of long bones, the growing line of cartilage is sheltered from the friction and stress to which it would be exposed if situated on the articular ends of the bones. All the cartilage of a bone, except that on the articular surfaces, is ossified when the body is fully grown. The evidence at our disposal points to both the absorption of the cartilage and the deposition of bone as being regulated by secretions derived from the thyroid, pituitary and other

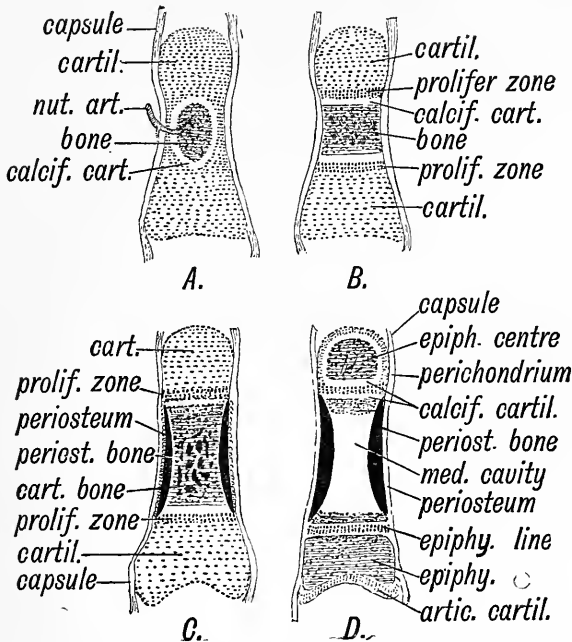


FIG. 478.—Ossification of a Long Bone by Endochondral and Ectochondral Ossification. (After Nicolas.)

- A, Ossification within the cartilage of the shaft.
- B, Complete ossification of the middle part of the shaft.
- C, Formation of bone in the shaft outside the cartilage by osteoblasts lying beneath the perichondrium (now named periosteum).
- D, Complete absorption of the endochondral bone of the shaft; formation of a medullary cavity; appearance of endochondral centres in the epiphyses; formation of the epiphyseal lines.

glands of internal secretion.¹ In the growth of a long bone, such as the humerus, the proximal and distal diaphyseal lines take an unequal share. Digby² found that while the proximal line added 4 parts to the length of the humerus the distal line contributed only 1 part. The chief nutrient

¹ Keith, *Lancet*, April 15th, 1911; *Journ. Anat.* 1913, vol. 47, p. 189; *ibid.* 1920, vol. 54, p. 101; *Lancet*, 1913, vol. 1, p. 305.

² Kenelm Digby, *Journ. Anat.* 1916, vol. 50, p. 186.

canal of the shaft of a long bone points to the centre at which endochondral ossification commenced.

Nature of Epiphyses.¹—Epiphyses are of three kinds: (1) pressure epiphyses, forming the articular extremities of long bones (Fig. 479, *B*); (2) traction epiphyses, which form processes for the insertions of muscles (Fig. 479, *B*); (3) atavistic epiphyses, formed by the union of an element which formerly existed as a separate bone (Fig. 479, *A*).

The upper extremity of the femur affords typical examples of pressure and traction epiphyses. By the extension of the ossification of the shaft within the cartilage of the upper extremity of the femur, the pressure and traction epiphyses become widely separated to form the head and trochanters. **Pressure epiphyses** are the first to ossify, their centres appearing in the order of their functional importance; they are always fitted to the shaft by a species of dovetailing to withstand dislocating forces. The

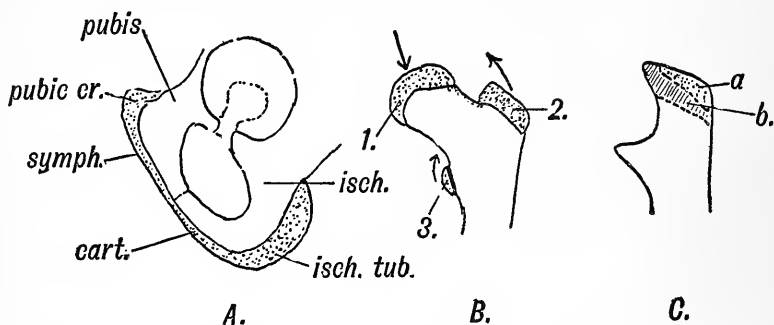


FIG. 479, *A*.—The Epiphyseal Cartilage of the Pubis and Ischium, which arises from the Median Cartilage of the Pelvic Girdle. (Parsons.)

B.—Traction and Pressure Epiphyses on the upper extremity of the Femur.

C.—The Epiphyses of the Olecranon: *a*, the usual Epiphyses; *b*, occasional Epiphyses: both *a* and *b* may be present. (Fawcett.)

upper extremity of the shaft of the humerus projects as a three-sided pyramid within the epiphysis; Professor Arthur Thomson has shown that the lower end of the shaft of the femur is fitted within its lower epiphysis by a number of projections not well marked in the human bone but pronounced in those animals which maintain the knee in a flexed position. Epiphyses are mammalian characters; their rudiments are to be seen in reptilia.

The great trochanter is the **traction epiphysis** of the gluteus medius and minimus; the small trochanter, of the psoas and iliacus; the third trochanter, in which a centre appears in the 20th year (Dixon), that of the gluteus maximus.

As examples of **atavistic epiphyses**, Parsons cites the following: those of the ischium and pubis (Fig. 479, *A*) from the median pelvic bar (Figs. 442, 479); the coracoid process; the epiphysis on the os calcis, the scale-

¹ The account given by Parsons has been followed. See *Journ. Anat. and Physiol.* 1903, vol. 37, p. 315; 1904, vol. 38, p. 248; 1908, vol. 42, p. 388. R. L. Moodie, *Amer. Journ. Anat.* 1907, vol. 7, p. 443 (Reptilian Epiphyses). A. Kirchner, *Anat. Hefte*, 1907, vol. 33, p. 513 (Epiphyses of Os Calcis and 5th Metatarsal). T. Walmsley, *Journ. Anat.* 1919, vol. 53, p. 326.

like epiphysis of the olecranon (Fig. 479, C). The internal and external condyles of the humerus may be derived from **sesamoid ossifications**, such as are now seen in the patellae, in the tendons of the popliteus, outer head of gastrocnemius (occasional), peroneus longus, tibialis posticus and at the metacarpo-phalangeal joints of the thumb and great toe. The **patella** is usually regarded as a sesamoid, but Mlle. Bertha Vriese collected evidence to show that it is really a true morphological skeletal element.¹

Lines of Pressure and Tension of Bones.—The trabeculae, in which the bony matter is deposited by the osteoblasts, are arranged so as to withstand the forces to which the body is subjected. When a bone, such as the astragalus, rib or neck of the femur, is laid open by a section, the trabeculae appear to form straight lines or septa which converge and meet at various angles; when, however, such bones are examined stereoscopically with the X-rays, the trabeculae are seen to be arranged in a double spiral—one system twisting from right to left, the other from left to right (Haughton and Dixon).² By this means, the greatest strength is obtained with the least expenditure of material.

Split Hand and Foot.—The extremities are subject to a remarkable series of malformations, which apparently represent arrests of their development. The digits may be abnormally short (brachy-dactyly), owing to an arrest in the differentiation of the blastema of the phalanges, the terminal phalanx being unseparated from the middle.³ Besides errors in the separation of the phalanges, there is an arrest of growth—usually in the middle phalanges, while, as Dr. Drinkwater has shown, extra phalanges may be intercalated. This is of frequent occurrence in the fifth digit of the foot. In another series of cases the hand or foot appears as if cleft—an appearance due in some cases to the fact that three or more of the digits on the ulnar side of the hand or fibular side of the foot have remained joined or webbed, as in the embryo of the 2nd month, while in others the condition is due to a splitting or dichotomy of the terminal plate of the limb bud. The condition is hereditary.⁴ In more extreme cases the digits on the radial, or more rarely, those on the ulnar side of the hand, may be absent; the corresponding bone of the forearm or leg is also undeveloped. Such cases lead one to suppose that the two distal segments of the limbs are developed from a radial and ulnar or tibial and fibular buds, and in such cases only one of these has been affected. Both may be arrested, the extremities terminating at the proximal segment. In extreme cases the limb buds are undeveloped.

¹ Bertha de Vriese, *Bull. de l'Acad. Roy. de Sc. Belgique*, 1909, March 27th.

² Dixon, *Journ. Anat. and Physiol.* 1910, vol. 44, p. 223.

³ A. Fischel, *Anat. Hefte*, 1909, vol. 40, p. 1; J. D. Fiddes, *Anat. Anz.* 1912, vol. 40, p. 544 (Supernumerary Hallux); J. Symington, *Journ. Anat. and Physiol.* 1906, vol. 40, p. 100 (Hyper-phalangism in Cetacea); H. Drinkwater, *Journ. Anat.* 1916, vol. 50, p. 177.

⁴ See T. Lewis, *Biometrika*, 1908, vol. 6, p. 25.

CHAPTER XXVIII.

SKIN AND ITS APPENDAGES.

Stages in the Evolution of the Skin.—We have already seen that the structures which are developed in the human embryo can be best explained by supposing that at one stage of evolution the ancestry of mammals lived and breathed in water. The skin of the human embryo until the end of the 2nd month of development is translucent, and has many points in common with that of the lowest gill-bearing vertebrates. It then consists of two layers—a deep or germinal, consisting of cubical epithelium and a superficial, made up of fattened cells (Fig. 481). In the 3rd month this superficial layer, known as the **epitrichium** or **periderm**, becomes horny in nature, recalling a stage which represents the evolution into a

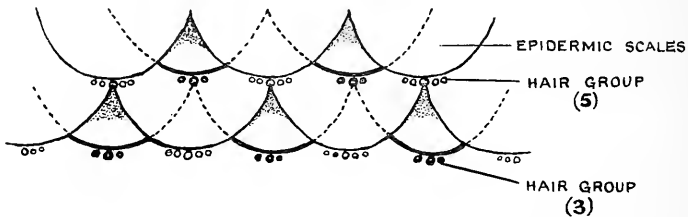


FIG. 480.—Showing the Arrangement of Hair Groups in the Human Foetus and their Relationship to Hypothetical Dermal Scales. (Stöhr.)

terrestrial form of life. The appendages of the skin—its hair and glands—appear later; they seem to be modifications of glandular and sensory structures seen in the soft skin of amphibia. The hairs are developed in groups and lines.¹ Their arrangement can be best explained, according to Dr. Max Weber, by supposing that the skin of primitive mammals was covered by scales, and that the hairs sprouted out in groups at their tessellated junctions, as in certain living edentates (see Fig. 480). The human hairs are arranged in irregular series, but in most instances only the chief hair of a group is developed. In later period of foetal life, however, the chief hair has one or two subsidiary hairs planted on either side of it—making one of a group of three or five hairs.

The skin of man, compared to other primates, is comparatively hairless. We must regard his nudity as a lately acquired character. At the 7th

¹ Stöhr, *Verhand. Anat. Gesellsch.* 1907, p. 153.

month of foetal life the chimpanzee and gorilla have hair only on the scalp, eyebrows and lips; the rest of the body is nude, except for fine hairs or lanugo. This is also the condition in the human foetus at a corresponding period; in man, although the foetal crop of lanugo is succeeded by a general outgrowth of fully developed hair, yet we may regard the human condition as representing an arrest of hair development at a stage seen in foetal apes. The human skin is also more sensitive and more richly supplied with sensory nerves than is the case in other primates. In Professor Elliot Smith's opinion the rich sensory supply to the skin must have been a factor in bringing about the large size of the human brain. In the distribution and "lie" of the hair on his body and limbs man also resembles the hairy anthropoids.

There are on record a number of cases of men and women, in whom the whole surface of the body was covered with a close covering of hair. The development of hair on the face is certainly regulated by a secretion derived from the sexual organs, for in eunuchs the beard is never developed. It is also well known that the thyroid has a direct influence on the development and growth of hair. Desquamation from the epidermis begins in the 3rd month of foetal life, and never ceases until death. In a certain disease of foetal life, named **Ichthyosis**, desquamation does not take place; the unshed epidermis forms cracked cakes on the surface of the child at birth.

Development of the Skin.—Considerable assistance in the understanding of the diseases to which the skin is liable and of the nature of the growths which arise from the epidermis, such as corns, bunions, and cancer, is to be obtained by studying the manner in which the skin is developed. At first the human embryo is covered by a single layer of epithelium (**epiblast or ectoderm**), as is the case in the adult amphioxus. By the end of the 1st month there are two layers, the lower representing the **germinal** or basal layer; the upper the **epitrichium**, so named because it was supposed that hairs are developed beneath it, and when they grew out in the sixth month this surface layer of flat epithelium was shed. This evanescent foetal layer is also known as the periderm.

In the 4th month we find developmental processes in full activity in the skin; three strata are recognizable in the epidermis—all derived from the single germinal layer. These are (1) a basal layer—a single stratum of cubical or columnar cells, representing the primitive germinal epithelium (Fig. 481, *B*); (2) an intermediate or mucous stratum, several cells deep; (3) a heaped-up superficial or corneous stratum, representing the protecting but perishing superficial covering of the skin. At the same time the opening phases in the development of hair follicles, sebaceous and sweat glands and of skin ridges and papillae are to be detected. In the 5th month the *stratum lucidum* becomes differentiated between the mucous and corneous strata.¹

The epidermis rests at first on undifferentiated **mesoderm**, consisting of small round cells closely imbedded in a mucoid matrix. This is the

¹ Comparative anatomy of epidermis: see F. K. Studnička, *Anat. Hefte*, 1909, vol. 39, p. 1.

normal structure of undifferentiated mesoderm. The superficial mesodermal cells are condensed beneath the epidermis to form a corium towards the end of the 3rd month; an areolar or subcutaneous stratum of tissue is differentiated at the same time. Connective tissue fibrils begin to develop in connection with the mesodermal cells and by the fifth month the mucoid substance has almost disappeared; but even in adult life, when the thyroid body is diseased or removed, a mucoid substance may reappear, and a condition resembling the foetal state be thus produced. In the mucous membranes of the lips, anus and vulva, the superficial layer of epithelium does not become cornified.

Formation of Dermal Papillae.¹—Up to the end of the 3rd month the epidermis is easily detached from the corium as a flat membrane, but early in the 4th month they become more closely united by ridges of epidermis becoming folded within corresponding furrows on the

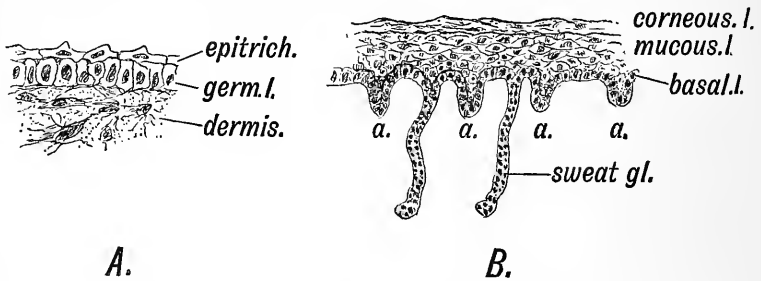


FIG. 481, A.—Diagrammatic Section of the Skin at the commencement of the second month.

B.—Diagrammatic Section of the Skin at the commencement of the fifth month. a. a. a. Infoldings of the epidermis between the primary ridges.

corium. About the 4th month, the dermal papillae, which are grouped in lines and ridges as is well seen in the palm, are formed in the following manner:

Long, linear furrows of epidermis grow down into the dermis (corium) and divide its surface into narrow ridges (Fig. 481, B). These ridges are subsequently subdivided into papillae. The down-growing nature of the ectodermal (epidermal) cells which is here exemplified, is of the greatest clinical importance. The enamel organs, we have seen, arose by a species of downgrowth of the epidermis; so do hairs, sweat glands and sebaceous follicles. Prolonged pressure and friction welds the corneous cells into a solid plate, such as the callosities seen on the palms of manual labourers. Normal desquamation is arrested; the cells produced in the deeper layers, unable to grow to the surface, grow inwards and produce corns. In cancer, the epithelial cells of the skin renew their youth and invade the dermis and deeper tissues.

¹ For literature see E. J. Evatt, *Journ. Anat. and Physiol.* 1907, vol. 41, p. 66. Also paper by Walter Kidd, same volume, p. 35. M. Heidenhain, *Anat. Hefte*, 1906, vol. 30, p. 419. O. Schlaginhaufen, *Ergebnisse der Anat.* 1905, vol. 15, p. 628. H. H. Wilder, *Amer. Journ. Anat.* 1901, vol. 1, p. 423. Walter Kidd, *The Sense of Touch in Mammals and Birds*, London, 1907; *The Initiative in Evolution*, 1920.

Sweat glands arise as buds from the ectodermal troughs (Fig. 481, *B*). Their ducts open on the surface of the skin in lines or rows corresponding to the primary epidermal furrows. In the 5th month the epidermis round their mouths is raised up into ridges, and it is these ridges which give rise to the papillary patterns on the balls of the fingers and elevations of the palm. It will be thus seen that the epidermal ridges correspond

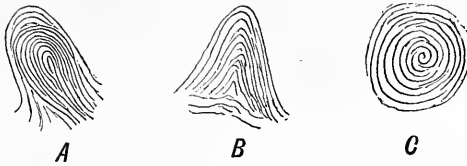


FIG. 482.—The more common patterns formed by the Dermal Papillae on the Tips of the Fingers.

A, The Loop Pattern. *B*, The Triangle Pattern. *C*, The Whorl Pattern.

not to the lines of **dermal** papillae, but to the furrows of epidermis lying between the papillae.

The papillary lines on the palms and fingers give security of grasp (Hepburn). They are arranged in most variable patterns, but the prevailing types in man are those arranged as loops, spirals or whorls (Fig. 482). So much does each pattern vary and so variable is the *sequence* of the patterns on the pulps of the digits, that no two people show exactly the same pattern in the same order counting from thumb to little finger

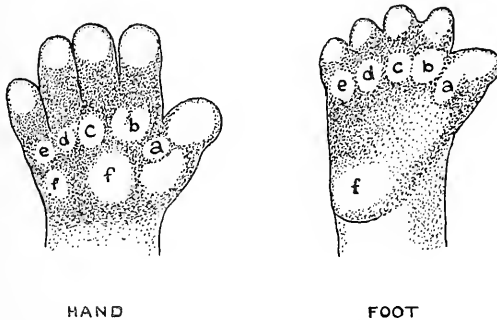


FIG. 483.—The "Pad" Elevations on the Palm and Sole of a Human Foetus at the end of the 2nd month of development. (After Retzius.¹)

in both hands. Hence the impress of the ten finger-tips has been successfully used in the identification of criminals—a practical discovery made and put into use by Sir Edward Henry.

These epidermal patterns² are formed on elevations which appear on the human hand and foot at the end of the 2nd month, and which certainly correspond to the horny pads found on the feet of quadrupeds. Besides the elevations on the terminal phalanges there are five situated on the palm and sole at the base of the digits. Three others are situated on the

¹ *Biolog. Untersuch.* 1904, vol. 11, p. 33, Jena.

² See references, p. 464.

proximal part of the palm. In the human foot the elevation corresponding to the hypothenar elevation of the palm undergoes a remarkable enlargement to cover the heel (Fig. 483).

The Hairs.¹—Hairs begin to develop in the 4th month, although in some regions, such as the eyebrows and lips, their formation begins a month earlier. Morphologically, a hair may be regarded as a dermal papilla which has sunk in the subcutaneous tissue, and become capped by a process of epidermis. Hairs appear to have been primarily touch organs, and are modifications of the touch bodies found in the skin of reptilia (Gegenbaur). These touch bodies are composed of epithelial cells, having the same shape and arrangement as those which form the taste buds in the circumvallate papillae of the human tongue. The cells which cap the hair papilla evidently represent the primary sensory cells of the touch

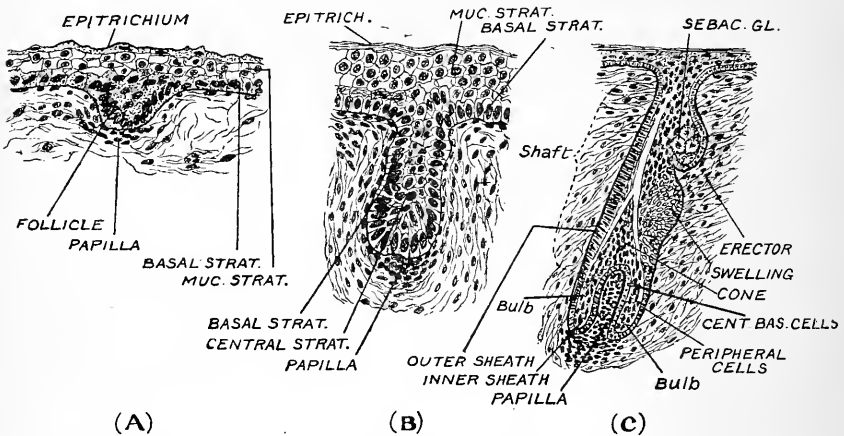


FIG. 484.—Three Stages in the development of a Hair Follicle. (After Stöhr.)

A, Hair Follicle, commencing to form in a Foetus of 3 months.

B, The downgrowth of the follicle and mesodermal thickening to form papilla.

C, Invagination of Follicular Bulb by Papilla with formation of Matrix Cone.

bodies; they are situated in line, and continuous with the basal or germinal layer of the skin. The primary function of the hairs as touch organs is seen in the vibrissae round the mouths of carnivora. Friedenthal has found that certain of the hair-roots in the lips and eyebrows of the human foetus develop the same large sensory bulbs as are found in the roots of the vibrissae of lower mammals.

The first stage in the development of a hair is the ingrowth of epidermis as a solid bud, which pushes in front of it the dermis to form the papilla on which the hair grows (Fig. 484). Only the two deeper of the primary layers of the epidermis are carried inwards to form the hair sheath and hair root. Three stages in the development of a hair follicle are shown in Fig. 484. As the follicle grows downwards the fundus of its shaft

¹ See Friedenthal, *Zeitschrift für Ethnol.* 1911, vol. 43, p. 974; K. Backmund, *Anat. Hefte*, 1904, vol. 26, p. 315; P. Stöhr, *Anat. Hefte*, 1904, vol. 23, p. 1; L. Stieda, *Anat. Hefte*, 1910, vol. 40, p. 285.

expands to form a bulb. Outside the follicular bulb mesodermal cells collect to become a papilla. Presently the bulb is invaginated by the papilla, which thus becomes clothed by the *central* cells of the basal stratum while the surrounding wall of the bulb is lined by *peripheral* basal cells. On the papilla and within the *shaft* of the follicle is produced a mass of cells—the hair cone (Fig. 484, C)—the first rudiment of a hair. The central cells on the papilla give rise to the cells which form the core or pith of the hair shaft; from the peripheral cells arises the inner root-sheath. The outer root-sheath is formed by the lining cells of the follicular shaft. As will be seen from Fig. 484, C, a sebaceous gland is produced from the shaft of the hair follicle, while the erector muscle arises from the shaft at a deeper level.

The hairs produced at the 4th month are fine in texture (*lanugo*), and by the 7th month the whole body is covered by them. The hair roots of the eyebrows, eyelids, and of the lips and scalp are the first to appear. The production of hair buds goes on until birth, the later buds and hairs being

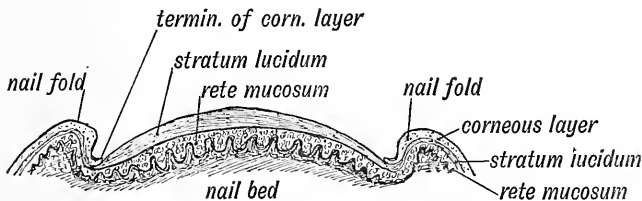


FIG. 485.—Diagrammatic Section across a Nail.

thicker and stronger. After birth, new hairs are constantly reproduced within the sheaths to replace the old. Probably the manner in which new hairs are produced resembles that of teeth, viz., from processes of the original bud. Hairs appear first on the head and then on other parts of the body. The fat in the subcutaneous tissue takes the place of hair as a heat conserver. Certain sexual hairgrowths appear at puberty on the face, pubes and axilla. Morphologically, the pubic region represents the separated axillary regions, and probably the explanation of sexual hairs in the axilla is due to this correspondence, for there is a persistent tendency towards symmetry of development in the upper and lower extremities. The primitive mammary ridges, also sexual structures, end at the axilla and groin.

Nails.—The nails are made up of three strata representing the basal layer of cylindrical cells, the stratum mucosum and the stratum lucidum of the skin, the corneous layer being lost after the 4th month of foetal life. They appear first in the 3rd month as fields of thickened epidermis on the tips of the digits (Fig. 473), but are afterwards shifted dorsally, carrying their palmar nerves with them, so that the terminal phalanx is wholly supplied from the palmar digital branches. At the end of the 3rd month the germinal layer of epithelium at the proximal margin of the nail field forms a lamina which grows into the dermis to form the root and is thus overhung by a reflection of skin—the *nail fold* (Fig. 486). The nail of the

little toe, a digit in a retrograde phase of development, is frequently shaped like a claw, probably a reversion to a primitive form. The nail is produced on the scattered papillae (the matrix) at its root. The area of production is marked by the lunule. On the nail bed, in front of the lunule, the papillae are arranged in longitudinal rows. If the nail be pressed, as by the boot, the lateral papillae, under the nail fold (see Fig. 485) are directed downwards, and their epithelial outgrowths follow the same direction, thus causing ingrowing nail.

About the end of the 7th month the matrix of the nail root becomes differentiated, active growth sets in and the terminal margin of the nail becomes free; it grows forwards over the corneous layer which covers the terminal row of papillae of the nail bed. The ridge of corneous epithelium

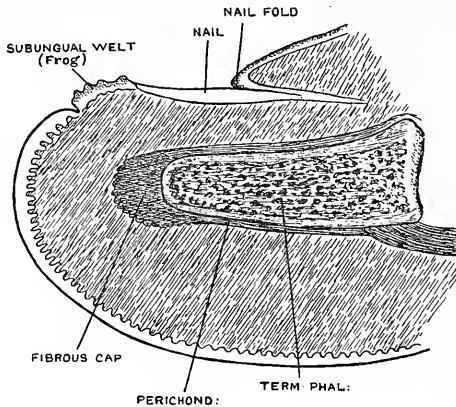


FIG. 486.—Diagrammatic Section of the Terminal Joint of the Digit of a Human Foetus to show the Cap of the terminal Phalanx and the Subungual Welt.

under the nail-tip represents the central part of the hoof ("frog") of ungulates (Fig. 486).

The nail is carried by the terminal phalanges. Professor Leboucq observed that the tip of the terminal phalanges of the foetus is covered by a special fibrous cap¹ (Fig. 486), which undergoes ossification directly from membrane, while the rest of the phalanx is laid down and ossified in cartilage. The terminal phalanges have thus a special element added to them for the support of the nail and for the fixation of the terminal bulb of the digits.

Sweat Glands.²—In the 4th month solid processes of epidermis grow into the dermis from the ectodermal troughs and also from the necks of hair follicles and produce sweat glands (Fig. 481, *B*). They arise at the same time and in the same manner as, and often in common with, the buds of hair roots and sebaceous glands. They are produced within the epidermal ridges, and hence the ducts of sweat glands, as may be seen on the

¹ F. A. Dikey, *Journ. Anat. and Physiol.* 1906, vol. 40, January.

² F. Diem, *Anat. Hefte*, 1907, vol. 34, p. 187; C. Schoeppler, *Anat. Hefte*, 1907, vol. 34, p. 429.

palms and fingers, open along the summits of these. The sweat glands in the axilla are peculiar. In section they resemble the acini of the mammary gland, also believed to be highly modified sweat glands. The axillary glands contain much epithelial debris. They appear to be sexual in nature. The wax glands of the external auditory meatus are also modified sweat glands.

Sebaceous Glands.—The sebaceous glands are outgrowths from the more superficial part of hair buds (Fig. 484). Their epithelial lining is derived from the germinal layer. In hair sheaths which have become occluded after their hairs have been shed or lost, or when the mouth of a gland is blocked, the secretion is retained, and a sebaceous cyst or wen, so frequently seen in the scalp, is produced. Round the mouth, on the lips and nose, the sebaceous glands, especially in disorders of the sexual organs, are apt to retain their secretions and become inflamed, small pustules being thus produced. The Meibomian glands in the eyelids are modified sebaceous glands. At birth the child is covered by the **vernix caseosa**, which is composed of desquamated corneous epithelium and the secretion of sebaceous glands.

MAMMARY GLANDS.

Evolutionary History.—It is a remarkable fact that although the milk glands do not come into use until adult life and although they must be regarded as among the later evolved structures of vertebrate animals, yet they are the first of all the glands arising from the epidermis to appear during development of the embryo. In the human embryo of the 6th week or in the corresponding stage of a pig (Fig. 487), or of any other mammal, the **primary mammary ridge** or milk line—a mere surface thickening of the ectoderm—is seen extending along the body wall on either side from axilla to groin. Breslau¹ regards these primary ridges as representatives of the brooding organs of the ancestors of mammals, from which structures he supposes that the mammary glands were evolved. In a large number of human beings (15 %) one or more supernumerary nipples are to be found between the axilla and groin, indicating the wide distribution of ancestral glands. There is no longer any doubt that the mammary acini and ducts have been modified from sweat glands; a mamma represents a group of sweat glands developed from a circumscribed area of skin lying under the primitive mammary ridge. Nor are there two opinions as to the stages in the evolution of the human nipple; they are repeated in its development. In its primitive form the nipple is represented by a pocket—an invaginated area of mammary skin—on the wall of which milk ducts open. This pocket—an inverted nipple—becomes everted, chiefly by a proliferation of the tissues round the terminal parts of the duct, which raises the interior of the pocket first to the level of the surrounding skin and then above it to form a nipple—an everted mammary

¹ *The Mammary Apparatus of the Mammalia*, with Introduction by Prof. J. P. Hill, London, 1920.

pocket. Further, the mammary ridge appears in both sexes alike, but this may not mean that both sexes of ancestral mammals were concerned in brooding or gave milk. The male is the father of girls as well as of boys; it is therefore necessary to provide both father and mother with a complete sexual outfit if each sex is to provide equal shares to the making of their progeny. In females the breasts undergo a great development at puberty, while in males they retain their infantile form.

The **Female Breast** is composed of two embryological elements: (a) Glandular tissue derived from the ectoderm by a process of inbudding; (b) An intricate arrangement of connective tissue derived from the mesodermal subcutaneous tissue over the pectoralis major.

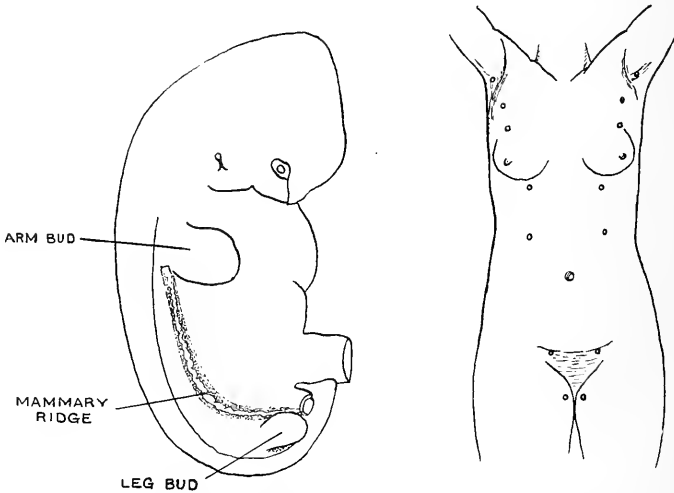


FIG. 487.—Embryo of a Pig, showing the Mammary Ridge extending from Axilla to Groin. (After Schultze.)

FIG. 488.—Diagram to show the Position in which Supernumerary Nipples are usually found. (After Merkel.)

Seven stages may be recognized in the developmental history of the **glandular mammary tissue**. Four of these take place **before birth**:

(1) The stage represented by the ectodermal ridge passing from axilla to groin—formed during the 6th week (Fig. 489, *A*).

(2) The production of a bulb-like downgrowth of ectoderm from the pectoral part of the mammary ridge. This downgrowth represents the pocket form of nipple (Fig. 489, *B*).

(3) From the deepest stratum of the ectodermal bulb arises a number of solid buds, exactly similar to those of sweat glands (5th month). The stalks of these buds form the epithelial lining of the lactiferous ducts (Fig. 489, *C*).

(4) The lobular buds, for each bud develops into a lobe, subdivide at their growing extremities. At first solid, they begin to canaliculize (7th to 9th months). At or about birth the pit or depression, from which the lobular buds originated, is raised, evaginated, and forms the surface of

the nipple (Fig. 489, *D*). Thus the ducts come to open on the apex of the nipple. An ampulla is developed in each duct within the base of the nipple. It is normal for the glandular tissue of the newly born child to secrete milk during the two weeks following birth (Roger Williams).

Stages after Birth.—Stage 5 occurs at puberty; the latent infantile lobular buds again undergo a rapid growth, and give rise to the minor lobules and acini. Stage 6 occurs towards the end of pregnancy, and consists of a renewed production of glandular tissue. Stage 7 sets in with the menopause, and is characterized by an atrophy of the glandular tissue formed in the later stages of development.

In the process of subdivision, minor buds of adjacent lobes frequently unite together. Hence it is found difficult, during dissection, to separate

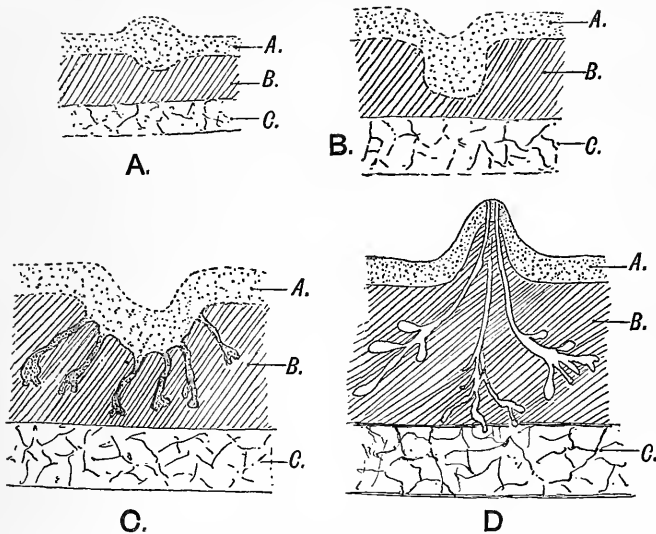


FIG. 489.—Showing the various Stages in the Development of the Mamma. *A*, during the 2nd month; *B*, at the commencement of the 3rd month; *C*, at the 5th month; *D*, at birth.

A = Ectoderm; *B* = Subcutaneous tissue (mesoderm); *c* = Pectoralis major.

the gland into its primary lobes. In any of the three later stages a localized and invading hypertrophy of the cells of the glandular tissue may take place. In this manner cancer is produced. The part played by the lymphatics, which are situated in the mesodermal tissue of the gland, in the spread of this disease, makes their study important.

Origin of the Capsular or Mesodermal Part of the Gland.—

As the glandular buds grow into the subcutaneous mesodermal tissue, which reacts and hypertrophies around the invading processes, they divide it (see Fig. 490), into (*a*) superficial, and (*b*) deep layers, these being joined together by (*c*) interstitial septa. The superficial and deep layers are fused in (*d*) the circum-mammary tissue in which the final glandular buds terminate. The processes as they grow outwards also take on (*e*) perilobular

and periductal sheaths. The deep and superficial layers are also connected with the anterior sheath of the pectoral muscles and the skin—for they are all parts of the same subdermal layer.

Lymphatics.—We have already seen (p. 337) that during the 3rd month the skin and subcutaneous tissues become invaded by the developing system of lymph vessels, the pectoral system lying chiefly in the zone arising in connection with the jugular lymph sac. As each part of the capsule carries with it lymph vessels of the pectoral subdermal area it will be seen that the arrangement of the parts of the capsule is an important matter in both the physiology and surgery of the gland. The **periductal** and **perilobular** lymphatics communicate through the **septal** or **interstitial** vessels with the **superficial mammary** and deep (**retro-mammary**) lymphatics (Fig. 490). The **superficial** communicate with

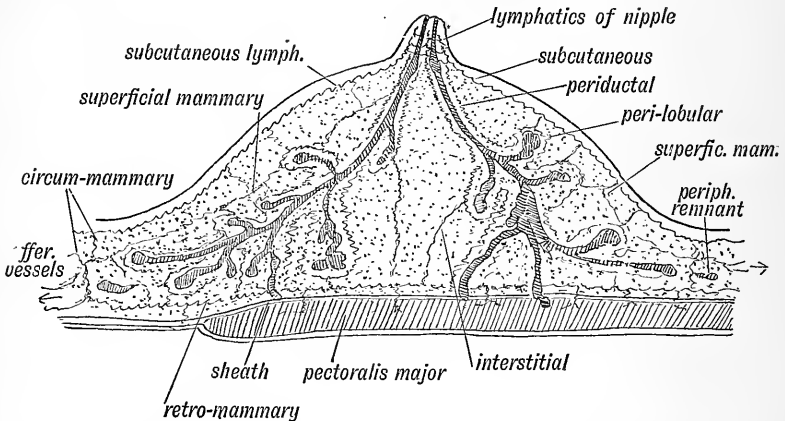


FIG. 490.—Diagrammatic Section of the Breast to show the Arrangement of its Capsule and Lymphatics. The lymphatic vessels are represented by thin wavy lines.

the **subcutaneous**; the deep with those in the **pectoral sheath**, and thus it will be seen that mammary cancer may spread to the skin or pectoralis major. The deep and superficial join in the **circum-mammary** lymphatics, and from these pass **efferent vessels** to the **pectoral** and **central** glands of the axilla. The lymph passes from these to the deep axillary and inferior deep cervical glands—all of which are involved in late stages of cancer of the breast. Other efferent vessels pass from the circum-mammary to the **anterior intercostal** glands of the upper four spaces; one or two vessels may go to the **cephalic** gland. During the mammary hypertrophy, which takes place at the end of pregnancy, there is a further formation of lymphatic glands in the axilla (Stiles).

Peripheral Remnants.—Besides accessory nipple ingrowths, which are to be found in most foetuses of the 3rd month, isolated or semi-isolated small masses of glandular substance may be found situated in the circum-mammary tissue, beyond the body of the gland. Some may pierce the sheath of the pectoralis major, and become a source of recurrent cancer.

The presence of glandular remnants is explained by the fact that, when the primary budding takes place, the subdermal tissue is shallow and of small extent; in the subsequent growth of the thorax, the tissue in which the mamma is developed is widely spread out.

Fat begins to be deposited in the subcutaneous tissue during the 5th month of foetal life. It forms a large element of the mammary gland after puberty. The subcutaneous tissue, out of which the capsule of the gland is formed, normally contains much fat. After lactation, when the glandular tissue atrophies to a considerable extent, a growth of fat replaces it. If no fat is deposited, or if it be absorbed, then the breast loses its plump form and hangs on the chest.

The mammary nerves (secretory) come from the 3rd, 4th and 5th intercostals; the nipple is supplied from the same nerves. The nipple contains non-striated muscle, and is covered with touch papillae, and surrounded by modified sweat and sebaceous glands.

Dermis and Subcutaneous Tissue.—The subectodermal tissues, out of which the dermis and subcutaneous stratum are differentiated, is at first composed of cells of rounded outline embedded in a homogeneous jelly-like matrix—a syncytium. Mall regarded the matrix as a living substance in which, quite independently of the cells, connective tissue fibres are differentiated, both white and yellow. Processes are certainly developed from the cells, but it is doubtful if these ever become detached and form independent fibres.

Fat Cells.—Certain granular cells of the connective tissue, especially of the subcutaneous layers, have the property of secreting **fat**, which appears first as diffuse droplets. These ultimately run together and produce the characteristic outline of adipose cells. Fat cells appear first in the subcutaneous tissue during the 5th month of foetal life; later it appears in the subserous tissue of the body wall. It reaches its greatest normal development just before and after birth. Two theories are held regarding the origin of fat cells: (1) that they are cells of the connective tissue differentiated and set aside permanently to form and store fat; (2) they are ordinary connective tissue cells temporarily laden with fat.¹ There is present at birth a sharply differentiated mass of fat and lymphoid tissue in each posterior triangle of the neck and extending on each side beneath the trapezius muscle. Hatai regards this mass as the representative of the **interscapular gland** of hibernating mammals (see p. 339).

Touch Bodies and Sense Organs.—The cells of the ectoderm in the simpler forms of invertebrate animals not only protect the body but many of them become specially sensitive or nervous in nature, developing processes which link them with neighbouring or even distant cells and thus are able to afford the animal knowledge of its surroundings. In the development of the olfactory mucous membrane, of the auditory cells and of the taste buds of the human embryo, this specialization of areas of the ectoderm is seen. The retina, the brain, spinal cord and nerves are also areas of the ectoderm which have been highly specialized and set aside for

¹ See article by Batty Shaw, *Journ. Anat. and Physiol.* 1902, vol. 36, p. 1.

the purpose of correlating the organism with its surroundings. Such cells may migrate and become grouped in central masses of the nervous system. Dart and Shellshear have shown that the dermal origin of neuroblasts is a factor of importance in the origin of the nerve system. Although the various forms of touch bodies, such as the Pacinian corpuscles and those of Krause and Meissner, have not been traced developmentally, there can be little doubt that they arise directly from the epidermis beneath which they are situated.

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